Factors affecting the availability of invertebrate food for the chough, *Pyrrhocorax pyrrhocorax* L.

David Ian McCracken
B.Sc. (Glasgow)

Thesis submitted to the University
of Glasgow for the Degree of
Doctor of Philosophy

Environmental Sciences Department
The Scottish Agricultural College
- Auchincruive
Ayr

September 1990

We often think that when we have completed our study of ONE we know all about TWO, because 'two' is 'one and one'. We forget that we have still to make a study of 'and'.

Arthur Stanley Eddington
(1882-1944)

ACKNOWLEDGEMENTS

Dr G N Foster deserves special thanks for his advice and guidance throughout this study - it was very much appreciated.

Thanks are also due to Dr E Bignal and S Bignal who provided an insight into the habits of the chough on Islay, and who also collected chough faeces on the island.

I am also grateful to all the farmers on Islay who allowed me access to their land.

This research was conducted while in receipt of a William Stewart Scholarship from the University of Glasgow. Facilities were provided by the Environmental Sciences Department of the Scottish Agricultural College - Auchincruive (formerly the West of Scotland Agricultural College). I should like to express my appreciation to Mr J W Newbold and all his staff (especially Mrs S Bone, Mr B Laird, Mrs K Crighton and Miss M Delaney) for their assistance and encouragement during the study.

Thanks are also due to the following: Dr S P Rushton, of Newcastle University, for initial assistance with the multivariate analysis techniques; Dr D Logue, of the Crichton Royal Farm, Dumfries, who allowed me to collect cow dung there; Dr D Ruthven & Dr K Hunter of DAFS - Agricultural Scientific Services, for developing the method used to extract ivermectin residues from dung; and Dr R Strang of the Biochemistry Department, University of Glasgow, for providing access to an HPLC machine.

I am extremely grateful to both the World Wide Fund for Nature (formerly the World Wildlife Fund) and the Environmental Sciences Department for meeting the expenses involved in travelling to and from Islay.

Mention must also be made of all my friends and colleagues, not mutually exclusive, at the College and elsewhere, who helped make the last three years an enjoyable experience.

Finally I must thank my parents and Miss R Strapp for suffering my moods during the write-up process - theirs was a very onerous task.

CONTENTS

LIST OF TABLES

LIST OF FIGURES

SUMMARY

Most of the fieldwork for this study was conducted on the island of Islay, in the Inner Hebrides, the stronghold of the chough, *Pyrrhocorax pyrrhocorax* L., in Scotland. The aims of this study were to provide baseline data on the phenology of potential invertebrate foods of the chough, and to provide a greater understanding of the factors affecting these invertebrate populations.

The literature concerning (a) the chough in Britain and its feeding ecology, (b) the invertebrate fauna of pasture, (c) the invertebrates associated with cow dung, (d) ivermectin and its effect on the invertebrate fauna associated with cattle dung, and (e) the multivariate analysis methods used in this study, is reviewed.

An area of heather moorland and four pastures were selected on Islay. Invertebrates were collected from these sites between January 1988 and November 1989 using pitfall traps, and by sampling soil and cow pats. The data obtained was analysed using two multivariate analysis methods - Two-Way-Indicator-Species-Analysis (TWINSPAN) and Detrended Correspondence Analysis (DECORANA).

Information on 62 surface-active taxa was obtained from pitfall trapping. Although seasonal taxa assemblages were recognized, the distribution of the invertebrate communities was primarily related to soil moisture content. Grazing intensity and seasonality were also important factors determining the composition of the invertebrate fauna at each site. The taxa active during the summer and winter at the two sand grassland sites, did not appear to differ as markedly as at the other sites sampled.

Figures showing the seasonal activity of some of the frequently occurring taxa at each site considered potential chough prey items are provided. Surface-active potential

chough food items were present, at all the sites investigated, throughout the year.

Soil-sampling provided information on 34 taxa. As with the surface-active fauna, the primary factor influencing the soil fauna was soil moisture content. The time of year was also an important factor governing the soil fauna composition, with the majority of taxa occurring in low numbers during the summer months at all the sites sampled.

Figures indicating the seasonal occurrences of some of the taxa considered potential chough prey items at each site are provided. Soil did not appear to be a good source of potential prey items for the chough during the summer months, although, as a result of seasonal increases in size, certain taxa, e.g. Tipulidae larvae, may have been more 'worthwhile' prey items at this time of year than at any other.

Information on 54 taxa was obtained from sampling cow dung. Seasonality and age of the dung were very important in determining the composition of the dung fauna.

The seasonal variations in the fauna associated with the cow pats are described. Potential chough prey items were associated with cow dung, in any stage of decay, throughout most of the year. Only during the period from October/November to January did there appear to be a lack of suitably sized potential prey items in the dung. The 'summer' months, when fresh dung contained large numbers of beetle adults and developing fly larvae, and late autumn, when pats deposited during the summer months are old enough for the large numbers of *Aphodius* spp. larvae present to have attained a reasonable size, were considered to be the times at which cow dung presented the best feeding opportunities for the chough.

Fifty taxa were identified in samples of chough faeces. Multivariate analysis of these data indicated that the seasonal availability of prey items was the most important factor influencing chough diet throughout the year. Soil-dwelling Tipulidae (January to July) and Bibionidae (January to April) larvae, dung-associated insects (during the spring, and late summer and autumn), and surface-active insects (during the summer) were important invertebrate components of the diet. Cereal grains were extremely important supplementary food items during the early winter months, when invertebrate availability was low.

An experiment was conducted at the College to investigate the effects on the dung fauna of spiking cow dung with 2.0, 1.0, or 0.5 mg/kg dung of ivermectin. Pats were placed on pasture between May and September 1988. The pats were lifted, and the soil beneath sampled, after 15 to 90 days exposure. A total of 65 taxa were identified.

These data were analysed using TWINSPAN, DECORANA and Canonical Correspondence Analysis (CANOCO). The major factors determining the invertebrate fauna of the pats were length of exposure, exposure date, and ivermectin presence/absence. Ivermectin markedly affected the fauna associated with the pats. Pats exposed in June and August degraded faster than those exposed in May or September. In June, the ivermectin-treated pats degraded significantly slower than the control pats.

An attempt to extract ivermectin from cow dung for analysis by high-performance liquid chromatography is described. This proved unsuccessful and the reasons for this failure, and possible improvements, are discussed.

The main conclusions of this study are:

(1) that Tipulidae larvae are extremely important components of the chough's diet on Islay, and that the climatic conditions of the island favour these insects;

(2) livestock farming on Islay, especially the out-wintering of cattle, provides essential feeding opportunities for the chough, as, (a) grazing animals produce the short sward preferred by the chough as a feeding habitat, (b) large numbers of insects are associated with the dung of these animals, and (c) supplementary feed provided for the cattle in winter also provides an essential alternative food source for the chough at a critical time;

(3) the chough's preference on Islay for feeding in sandy, coastal pasture is due to the fact that these sites, (a) contain a variety of suitable invertebrate prey items throughout most of the year, (b) are normally intensively grazed and so contain large amounts of dung with its associated fauna, and (c) are used for out-wintering cattle and therefore cereal grains can be found there;

(4) treating cattle with ivermectin could have an adverse effect on the chough as it reduces the number and variety of invertebrates associated with the dung, an important food source for the birds, especially in spring and autumn.

CHAPTER ONE: GENERAL INTRODUCTION

The chough, *Pyrrhocorax pyrrhocorax* L., is the rarest member of the crow family, the Corvidae, breeding in Britain. It does, however, have an extensive global distribution, although its occurrence is local and patchy throughout its range. It is found in much of southern Europe, with scattered populations in Iberia, along the northern Mediterranean area, in Brittany and on the west coast of Britain. It also occurs over much of central Asia to the Himalayas, with more isolated populations present in Morocco, the Canary islands and Ethiopia. Several different races of choughs have been recognized and classified as sub-species, but the differences between these are few. The nominate race, *P. p. pyrrhocorax*, is restricted to the British Isles and Brittany (Monaghan, 1988a).

In Britain, the chough is essentially a coastal bird and is confined to the western seaboards of Ireland, Scotland and Wales (Monaghan, 1988a). In the past it was much more widespread, but declined throughout the eighteenth and nineteenth centuries and is now completely absent from England; its distribution in Scotland and Wales is very limited compared to former times. The reasons for its decline in numbers and the contraction of its range are not well understood, but may include persecution, collection, changes in land use and climatic factors. In Scotland, the northern limit of the chough's distribution, breeding birds have been confined to the Inner Hebrides and the Mull of Kintyre since at least the 1930s, and Islay has been the major stronghold for many years (Monaghan *et al.*, 1989).

In recognition of its rarity and the need for active conservation measures, the chough has been placed on Schedule 1 of the 1981 Wildlife and Countryside Act for

Britain, and, in 1985, on Annex 1 of the European Community Directive on the Conservation of Wild Birds. The latter confers a responsibility on member States to conserve both the bird and its habitat.

On the island of Islay, in the Inner Hebrides, long-term research into the biology of the chough is being conducted by the Nature Conservancy Council and the University of Glasgow. The aims of the present study were to provide baseline data on the phenology of potential invertebrate foods of the chough, and to provide a greater understanding of the factors affecting the distribution of these invertebrate populations. Such information is essential to establish (a) why Islay remains a stronghold for the chough, and (b) what land-use changes might threaten this status. In view of the conflict on the island between farming and conservation, the study was conducted at 'arm's length' i.e. the research concentrated on the invertebrates rather than the chough. This study was intended to complement the long-term investigation, and it was hoped that the results obtained would help the formation of policies to meet the requirements of the above legislation, and therefore aid the conservation of the chough in Britain.

The literature is reviewed in Chapter 2. Chapter 3 describes the sites and sampling methodology on Islay, and the results obtained from pitfall trapping, soil sampling and sampling cow dung at these sites are presented in Chapters 4, 5 and 6, respectively. Faecal analysis is used in Chapter 7 to investigate the chough's diet throughout the year. An experiment to assess the effect of ivermectin (a drug used in animal health) residues in cow dung on the associated invertebrate fauna is presented in Chapter 8. An attempt to extract ivermectin from cow dung is described in Chapter 9. A general discussion of the study is provided in Chapter 10.

CHAPTER TWO: LITERATURE REVIEW

(a) The chough in Britain and its feeding ecology

The chough population

Prior to 1982 the chough in the British Isles had never been adequately surveyed. The only previous attempt at a comprehensive census was in 1963 (Rolfe, 1966), and, although often quoted, the accuracy of this survey is debatable.

In 1982 a survey was organised to determine the breeding numbers and distribution of the chough in Britain and Ireland, and to collect data on the habitat types within the main breeding areas. This survey located a total of 905 breeding pairs. This was a minimum figure, which represented probable plus definite breeding pairs. The bulk of them were in Ireland (656-685 pairs). Wales held 139-142 pairs, Scotland 61-72 pairs and the Isle of Man 49-60 pairs. In addition, about 825-858 non-breeding birds were encountered (Bullock *et al.*, 1983).

The total Scottish population in 1982 was estimated to be between 171 and 211 birds, with about 83% occurring on Islay (Warnes, 1983). In 1986 a second, and the most recent, Scottish survey estimated the minimum population to be between 325 and 340 birds, of which 90% were on Islay. Although not directly comparable, the 1982 and 1986 survey results were sufficiently different to indicate that the population had increased. However, the concentration of the population in such a small area makes it particularly susceptible to changing circumstances. It has been stated that a better understanding of the chough's population structure, behaviour and ecological requirements is needed to help to frame a conservation policy for the bird

(Monaghan *et al.*, 1989).

Chough feeding ecology

Despite its rarity, few studies of chough biology have been made in Britain. Bullock (1980), Roberts (1982) and Warnes (1982) studied chough feeding ecology and behaviour on South Stack (Anglesey), Bardsey Island (Gwynedd) and Islay, respectively.

Bullock (1980), working on Anglesey, confirmed that the chough digs in the soil for its food, and exploits seasonal abundances of certain invertebrates. In winter (November-February) the birds took beetles, especially *Cylindrinotus laevioctostriatus* (Goeze), and their larvae in heathland peat. Barley grains were also important at this time. During the breeding season (April-June) *C. laevioctostriatus* adults continued to be taken, along with other surface active beetles, and swift moth (*Hepialus* spp.) and crane fly (Tipulidae - *Tipula* spp.) larvae. Early in the post-fledging period (July-August) the birds moved from feeding on heathland to feeding around cliffs. Consequently ants, *Formica* and *Myrmica* spp., prevailed in the diet at this time, along with a variety of surface-active beetles and spiders. From August to October the birds gradually returned to feeding on the heathland.

Bullock (1980) also suggested that mere abundance of invertebrates was not enough, and that good chough feeding sites must either have a modicum of bare ground or vegetation short enough to allow access to the soil for digging. Thus, maritime heathland which is periodically burned, maritime turf or short-grazed traditional rough pastures should all be ideal feeding habitats, since each has minimal vegetation cover and is rich in invertebrates. To test these ideas, the 1982 population survey also recorded the proportions of habitats available in all the areas visited, and the habitats selected by feeding chough.

The results showed that rough, unimproved pasture grazed by sheep or cattle was an important feeding habitat in all the areas surveyed in Britain and Ireland, and that maritime turf and machair (low-lying dune grassland) were also selected by feeding birds (Bullock *et al.*, 1983).

Roberts (1982) investigated the seasonal changes in the chough's diet on Bardsey Island, north Wales, over a nine month period from March to November 1979. He found that between April and June, beetle larvae (Carabidae, Staphylinidae and Scarabaeidae) were important in the diet, along with crane fly, *Tipula* spp., and swift moth, *Hepialus* spp., larvae. During the summer months (July-September), ants assumed importance in the diet, along with surface-active beetle adults and spiders. From September to November, dung beetle (Scarabaeidae - *Aphodius* spp.) adults occurred in chough faeces. Kelp fly, *Coelopa* spp., adults and larvae, and sandhoppers, *Orchestia* spp., were also taken when the birds fed on beaches in October and November.

Warnes (1982) found that, in all seasons on Islay choughs preferred to feed on short pasture grazed by cattle or sheep. *Aphodius* spp. remains were found in adult chough faeces on Islay throughout the year, but especially during the winter (October - March) when between 30 and 74% of the faeces from flock feeding birds contained dung beetle adults, and between 3.7 and 61% contained larvae. Cereal grains were also an important component of the diet at this time. During the spring and summer (April - September) *Aphodius* spp. adults and larvae were the most frequently occurring prey items in chough faeces, although a greater variety of other prey items e.g. fly larvae, and other beetle adults and larvae, were also taken. Analysis of nestling faeces in May and June also showed *Aphodius* spp. beetles to be the most frequently occurring prey items. She concluded that, although adult choughs appear to exploit a wide variety of prey items, *Aphodius* spp. beetles and their larvae were important components of the chough's diet on Islay throughout the year.

As part of their study of land use and birds on Islay, Bignal *et al.* (1988) considered the relationships between the chough and its environment. They reported that the majority of summer and winter sightings of chough were in some form of grassland vegetation (58 and 63%, respectively), with the highest proportion in species-poor grassland during the breeding season and in species-rich grassland in the winter. Species-poor grassland included permanent pastures on raised beach terraces as well as rough hill grazing. Over 50% of these grasslands were grazed by cattle, with both sheep and red deer also present. The species-rich grasslands were also heavily grazed, with over 26% holding cattle and 73% holding sheep. These species-rich swards were developed over limestone or blown sand.

Of the eight land-types identified during the study, choughs showed a preference for rocky coasts and coastal cliffs, farmland, and coastal pasture in both summer and winter. Sandy coast was not used preferentially during the summer but it did feature during the winter. Although no strong preference was shown for them, two other land-types were also used by choughs: broken moorland and rough pasture, and bogland.

In addition to the detailed studies above, a number of short-term studies or compilations of observations have been reported, e.g. Holyoak (1967) described the feeding actions of the chough on the Calf of Man, and predicted that earthworms, moth larvae and Tipulidae larvae were taken; Cowdy (1973) reported that between late June and early July the diet of chough on Ramsey Island, south Wales, consisted almost entirely of ants; Gatehouse and Morgan (1973) observed chough feeding on adult beetles associated with sheep dung in Wales; and Smiddy (1986) in Ireland recorded chough feeding on moth larvae found on top of dense vegetation.

(b) The invertebrate fauna of pasture

A great variety of invertebrates are associated with grasslands. The following, largely extracted from Curry (1987a, b & c), concerns only those groups of soil-dwelling and surface-active invertebrates considered to be potential chough prey items.

Oligochaeta: earthworms (Lumbricidae) are most prominent in fertile, free-draining, base rich mineral soils of adequate moisture status and with pH approaching neutral (e.g. Nordstrom & Rundgren, 1974); populations are limited by unfavourable moisture conditions, low pH or unsuitable food in arid soils and moorland and heathland (e.g. Curry & Cotton, 1983). Spring and autumn peaks in earthworm abundance and activity are typical of temperate soils, reflecting favourable temperature and moisture conditions and food supply (e.g Persson & Lohm, 1977). Earthworms play a major role in creating and maintaining soil fertility through litter ingestion, burrowing and soil mixing (Curry, 1987c).

Myriapoda: centipedes (Chilopoda) are predominantly associated with moist woodland but are also common in grassland. They are primarily carnivorous, feeding on soil and litter invertebrates, although significant amounts of plant material have also been reported in gut contents. Millipedes (Diplopoda) are also primarily woodland animals which can be abundant in rough grassland. They are mainly saprophagous, and play a role in the fragmentation and decomposition of plant litter (Curry, 1987a).

Araneae: spiders reach their greatest abundance and species diversity in unmanaged grasslands, where the complex vegetation provides suitable sites for web attachment by a range of species. Short, managed swards usually have low abundances and species diversity. Small, surface-dwelling Linyphiidae are usually the dominant group, particularly in managed grasslands (e.g. Luff & Rushton, 1989; Rushton *et al.*, 1989). Spiders are carnivorous, the main prey of web spinners being Diptera, Hemiptera, Acridoidea and immature spiders (Curry, 1987a).

Coleoptera: a wide range of species occur on the soil surface and low vegetation (e.g most Carabidae and Staphylinidae), while some are true soil-dwellers for all or part of their life cycles (e.g many Elateridae). Surface-dwelling Carabidae and Staphylinidae are mainly predatory, feeding on Collembola, Diptera, Coleoptera, Aphidoidea, earthworms and other prey (e.g. Sunderland, 1975; Luff, 1987). Predatory Cantharidae and Histeridae are also common in grassland. Some Silphidae, Dermestidae, Cleridae and Tenebrionidae are associated with decaying carrion, while many Geotrupidae and Scarabaeidae are coprophagous (see Section (c)). However, the majority of grassland beetles are saprophagous with unspecialised feeding habits (Curry, 1987a).

Diptera: dipterous larvae are most abundant in moist organic habitats and scarcest in arid soils (e.g. Persson & Lohm, 1977). Most grassland Diptera belong to the suborder Nematocera, the commonest families being Tipulidae, Bibionidae, Mycetophilidae, Cecidomyiidae and Chironomidae. Although some Tipulidae and Bibionidae larvae may feed on grass roots, the majority of nematoceran larvae are saprophagous, and are particularly associated with accumulations of organic matter, including dung. Soil-dwelling Brachycera larvae such as Stratiomyidae, Empididae and Dolichopodidae are mainly predacious, and Cyclorrhapha larvae are common in rotting vegetation and dung, with some Anthomyiidae, Scathophagidae, Sepsidae and Sphaeroceridae being primary colonizers of fresh dung (see Section (c)) (Curry, 1987a; Smith, 1989).

Hymenoptera: ants (Formicidae) tend to be most abundant in open forest and dry, uncultivated grasslands. European grassland species feed mainly on small invertebrates and Aphidoidea honeydew (e.g. Curry, 1987a).

Lepidoptera: the larvae are all phytophagous. Populations in grassland are generally low, but a number of species can be abundant e.g. swift moth larvae (*Hepialus* spp., Hepialidae) (Curry, 1987a).

Dermaptera: earwigs are omnivorous, feeding on a wide range of both living and dead animal and vegetable material, and may be important aphid predators when abundant (e.g. Brindle, 1977; Sunderland & Vickerman, 1980).

Curry's (1987b) conclusions are given below.

(a) The structure and composition of the grassland sward greatly influence the the invertebrate community, with swards that are rich in species, and which have a complex physical structure, supporting an abundant and diverse fauna.

(b) Climate and weather have a major role in determining occurrence, life history, phenology and population ecology of grassland species.

(c) Soil physical and chemical characteristics such as organic matter content, pH, soil moisture and temperature influence the above-ground fauna indirectly through the vegetation, and influence the soil fauna in a more immediate way.

(d) Management practices greatly influence sward structure, composition and productivity and induce corresponding changes in the invertebrate community. In intensively utilized grasslands, the complex communities of unmanaged swards are replaced by highly simplified communities of species which can tolerate disturbance and which can exploit the increased productivity. Grazing, cutting, fertilizer use, soil water control and pesticide application are the management practices which most affect the fauna.

Southwood (1987) considered the suggestion (as shown by Curry's conclusions) that the great variety of properties exhibited by communities may be codified by reference to the features of the habitat. He suggested that the communities associated with any habitat were determined by two main selective gradients: that of *r-K* selection, and that associated with adversity.

He stated that the *r-K* selection gradient was a reflection of the habitat's durational stability i.e. the period of time (in generation time) during which the habitat remains suitable for the organisms that live in it, and suggested that disturbance (a physical force that reduces the biomass of a habitat) was the main determinant of this durational stability. He also maintained that the adversity gradient (alternatively termed the selection for tolerance to stress) was determined by a combination of temperature and moisture, or some other physical conditions, that are sub-optimal for biological processes.

He suggested that a third variable important in the description of a community's habitat was the variation in the climatic conditions i.e. the extent of seasonality and its predictability.

Some examples of recent investigations of the invertebrate fauna of pastures are given below.

Luff & Eyre (1988) assessed Curculionoidea communities in grassland, and concluded that community structure was determined primarily by soil moisture and drainage, and secondarily by plant species composition and the level of management of the site.

Morris & Rispin (1987) investigated the abundance and diversity of Coleoptera on a calcareous grassland under different cutting regimes, and found that the treatments had considerable effects on the beetle fauna, reducing the diversity of species present.

Luff & Rushton (1989) sampled the Carabidae and Araneae fauna of managed and unmanaged upland pasture, and suggested that pasture improvement had a more drastic effect on ground beetle and spider communities than did subsequent pesticide use.

The results obtained from sampling the Carabidae and Curculionoidea fauna on grassland sites differing in intensity of management also indicated that management was the most important factor affecting the communities (Eyre *et al.*, 1989).

Eyre *et al.* (1990b) investigated the Carabidae fauna of intensively managed agricultural grasslands, and found that substratum conditions, especially soil water and soil density, were important in influencing community distribution.

Referring to Southwood's concept, the examples given above would suggest that perhaps the main 'disturbance' factors determining grassland invertebrate communities are related to management practices, e.g. the grazing and cutting regimes, and that the main 'stress' factors involved are related to some feature of the soil, especially soil moisture and density, although other factors (e.g. aspect, altitude and latitude) must surely also be important.

(c) Invertebrates associated with cow dung

Dung ecology

Most published studies of dung communities fall into one of three categories (Doube, 1987). These are studies of:

(1) species composition and successional processes for guild(s) (defined as a group of species which exploits the same class of environmental resources in a similar way - Root, 1967) or entire communities (e.g. Mohr, 1943; Valiela, 1974; Koskela & Hanski, 1977);

(2) the seasonal and habitat associations and behaviour of species from guilds within the community (e.g. Hammer, 1941; Landin, 1961);

(3) the feeding and reproductive biology of coprophagous and predacious species (e.g. Holter, 1974; Hanski & Koskela, 1977; Putman, 1983).

Dung communities are characterized by abundant aerobic and anaerobic (e.g. rumen bacteria) micro-organisms, a diverse arthropod fauna, and an array of vertebrates, e.g. scavenging birds and mammals (see Putman, 1983). Apart from micro-organisms, the majority of species and individuals belong to the orders Coleoptera, Diptera, Hymenoptera and Acarina (Doube, 1987).

The trophic relations in dung pats are similar to those in other heterotrophic systems, e.g. rotting logs or leaf litter. There are primary consumers, e.g. fly larvae and dung beetles, which consume dung bacteria, and secondary and tertiary consumers, e.g. predatory beetles, which prey upon the primary and secondary consumers. However, these categories are not mutually exclusive for there are species of primary consumers which are facultative predators, e.g. some Muscidae fly larvae, and other species which act as primary and secondary consumers at different stages in their life-cycle, e.g. some Hydrophilidae beetles have coprophagous adults and predacious larvae (Doube, 1987).

Within the primary consumers there are guilds whose members consume dung juices, e.g. Muscidae fly larvae and Staphylinidae beetles, or dung juices and dung fibre, e.g. Scarabaeidae dung beetles. There are also guilds of secondary consumers consisting of predators of immature flies (e.g. mites, fly larvae, Staphylinidae beetles and larval Hydrophilidae) and pupal parasitoids, e.g. 'micro-Hymenoptera' and aleocharine Staphylinidae beetles (Doube, 1987).

Fauna associated with cow dung

Desière (1973), working in Belgium, considered that, whatever the time of year, cow dung is the centre for four large waves of invasion.

(1) As soon as it is deposited, cow dung is attractive to numerous species of adult Diptera, the majority of which are searching for a site to deposit their eggs. Their peak of abundance usually occurs a few hours after deposition of the dung, and their disappearance is due to the formation of a crust on the dung, through which it is difficult for them to lay their eggs.

(2) A second wave of invasion occurs with the arrival of large numbers of adult coprophilic Coleoptera, essentially belonging to five families: Hydrophilidae, Staphylinidae, Scarabaeidae, Histeridae and Ptiliidae. These beetles generally attain their maximum density between the first and the fifth day after deposition. Therafter their populations dwindle, and they are practically non-existent in 15-25 day old dung.

(3) The arrival of the beetles in the dung is the starting point for the third wave of invasion. This consists of nematodes and mites, the majority of which are carried by the beetles, who they leave as soon as they enter the dung. Their appearance in numbers begins about the tenth day and is extended for several weeks.

(4) Finally, in the later stages of dung decay, the

ecological barrier that existed between the dung and the soil underneath progressively disappears, allowing the introduction of important soil species such as springtails and earthworms. It is through this fourth, and last, wave of invasion that the process of humification of the dung occurs.

Nematodes and mites are not large enough to be potential chough prey items. Therefore this account concerns only Diptera, Coleoptera and earthworms.

In the temperate regions, the major investigations of the invertebrate fauna of cow dung have been carried out in Scandanavia and North America. Even though some of these were conducted up to 50 years ago, they remain authoritative works in this field.

Hammer (1941) conducted a very complete study of the Muscidae and other flies associated with cow pats in Denmark. A succession of species of ovipositing flies with ageing of the pat was described. He concluded that a number of factors restricting propagation influenced life in the pat. The most important factor reducing the fly population was predation on the fly larvae by the beetle inhabitants - Histeridae, Hydrophilidae and Staphylinidae. For most of the fly species studied, the influence of the weather, competition, and attack by predatory dipteran larvae and parasitoids were of minor importance.

Mohr (1943), working in the United States, described the fly and beetle inhabitants of cow pats, and used the terms 'microhabitat' for the pats and 'microsere' for the succession of species found in the microhabitat. He recognized several key factors: (1) most species present in the beginning of succession were specialists, i.e. obligatory dung breeders, whilst those appearing during the later stages were frequently microhabitat generalists; (2)

a dropping was likely to be inhabited by fewer species as it aged; (3) the earliest species in the succession tended to have the shortest life histories and the shortest occurrence in the pats; (4) succession was faster in the early stages; and (5) the environment of the dropping had a profound influence on the pattern of succession.

Landin (1961) studied the ecology of dung beetles (Scarabaeidae: Aphodiini) in Sweden. He found that dung beetles could be grouped into three categories: (a) 'eurytopic species', inhabiting dung pats in all kinds of localities; (b) 'oligotopic species', preferably, but not exclusively, living in a certain kind of habitat; and (c) 'stenotopic species', restricted to a certain kind of habitat. He discovered that the distribution of dung beetles in different habitats, e.g. open pasture compared to forest, did not depend on the type of dung available, e.g. sheep, cow, horse, but on the climatic conditions of the environment, especially the microclimatic conditions of the pat.

Valiela (1974) studied the structure of cow dung communities in the United States. He found that, invertebrates invaded the dung in an orderly pattern and the the number of taxa and the complexity of the food web increased as succession occurred. Short-term, local changes in the environment during early succession appeared to have a more pervasive effect on species abundance than seasonal changes. He concluded that compet~~et~~ition for dung was not likely to be a major limitation for dung-feeding populations. Predation did not appear to limit prey populations, nor did the predators appear to be prey-limited. He suggested that local, short-term changes in dung and the immediate environment may be too fast and too eratic to permit fuller use of dung as a resource.

Research on the annual dynamics of insects in cow pats has also been conducted by Merritt & Anderson (1977) in the United States, and more recently Koskela & Hanski (1977), Hanski & Koskela (1977), and Hanski (e.g. 1980a, b, c & d; 1986) have studied the ecology of coprophagous beetles in Europe. In addition, Holter (1977 & 1979), working in Denmark, has confirmed the importance of earthworms with regard to the disappearance of cow pats from pastures.

Work in Australia should also be mentioned. There, kangeroos were the primary producers of herbivore dung prior to European settlement. Since then, kangeroos have been largely replaced by cattle, horses and sheep which graze the extensive pastures that have replaced the bushland. The original Australian dung fauna was dominated by beetles adapted to a bush environment and to marsupial pellets, but ill-adapted to dealing with bovine dung in a grassland environment (Waterhouse, 1974). Bovine dung was therefore poorly colonized by indigenous dung beetles and provided an ideal breeding medium for coprophagous flies, which, in many regions, became the dominant element in the dung pat fauna. Exotic dung beetles and predators are therefore being introduced to Australia in an attempt to reduce the numbers of dung-breeding flies (Bornemissza, 1976; Doube *et al.*, 1988).

Very little research has been carried out on the invertebrates associated with cow dung in Britain. With the exception of Laurence (195~~1~~2), in his investigation of the larval inhabitants of cow pats, and Denholm-Young (1978), who studied the fauna associated with decaying cow dung, most studies have been conducted at an individual family or species level (e.g. Parker, 1970; Pitkin, 1988).

Finally, it is interesting to note that many of the above studies recorded birds as important predators on the invertebrates associated with the cow pats, e.g. jackdaws broke up and scattered cow pats throughout the year in their search for food at Rothamsted (Laurence, 1954).

Kumar & Lloyd (1976) provide a bibliography of the arthropods associated with dung, and Putman (1983), Doube (1987) and Skidmore (1989) should be consulted for more detailed information on this topic.

(d) Ivermectin and its effect on the invertebrate fauna associated with cattle dung

The chemical

In 1979 the discovery of a new class of macrocyclic lactones with broad spectrum agricultural pesticidal activity was reported (Burg *et al.*, 1979; Miller *et al.*, 1979; Egerton *et al.*, 1979). These compounds, collectively referred to as avermectins, were isolated from a fermentation broth of the soil actinomycete *Streptomyces avermitilis*, discovered by the Merck, Sharp and Dohme (MSD) Research Laboratories during routine screening of microbial extracts from Japanese soil.

Initially they were found to be extremely potent anthelmintic agents, demonstrating potencies in the range of 10-300 parts per billion (mcg/kg body weight) when administered to sheep, cattle, dogs and poultry infected with a spectrum of common gastrointestinal parasites (Egerton *et al.*, 1979). Subsequent research demonstrated potent insecticidal activity against a range of veterinary ectoparasites, agricultural and household insect pests of several orders, and phytophagous mites (Campbell, 1985).

The avermectin complex consists of four major components (designated A_{1a}, A_{2a}, B_{1a} and B_{2a}) and four minor homologous components (A_{1b}, A_{2b}, B_{1b} and B_{2b}). Mixtures of the homologous substances containing approximately 80% or more of the 'a' and 20% or less of the 'b' components, are usually referred to as avermectins A_1, B_1, A_2 and B_2. Of these four mixtures, avermectin B_1 (or abamectin as it is now known) is the most potent broad spectrum anthelmintic and has more activity against most of the arthropod species tested. It was therefore selected for further investigation and development.

Ivermectin (22,23-dihydroavermectin B_1) is a synthetic derivative of abamectin developed for animal health use. It was introduced into the international animal health market place in 1981. In Britain it is approved for use in cattle, pigs, sheep, goats and horses. The drug is absorbed systemically after oral or subcutaneous (s.c.) administration, but is absorbed to a greater degree when injected subcutaneously. From studies with radiolabelled ivermectin it appears that the drug is mainly excreted in the faeces of treated animals, with less than 1% excreted in the urine (Campbell, 1985).

Like its precursor, abamectin, the efficacy of ivermectin appears to be limited to nematode, insect and acarine parasites. Against nematodes and arthropods, ivermectin is extremely potent - the effective dose is invariably a fraction of a milligram per kilogram of body weight. It is roughly equipotent against nematodes whether given orally or parenterally (administration other than via the alimentary canal), but for some ectoparasites, such as mange mites, s.c. injection is more effective than oral treatment (Campbell, 1985).

Ivermectin is used to treat cattle in Britain primarily as a liquid for s.c. injection, although a topical (dermally applied) formulation is also available. **Ivomec** is a sterile solution, containing 1.0% w/v ivermectin in a mixed solvent vehicle of 60% (v/v) propylene glycol and 40% glycerol formal. It is designed to be injected subcutaneously at a dosage of 1 ml per 50 kg body weight (b.w), corresponding to 0.2 mg active ingredient (a.i.)/kg.

The effect on the dung fauna

An added advantage to antiparasitic treatment of an animal with ivermectin, is that, following treatment, the faeces may contain enough drug to prevent development of certain pest species of fly larvae (Meyer *et al.*, 1981; Miller *et al.*, 1981; Schmidt & Kunz, 1980; Schmidt, 1983), and the blood may contain enough to kill some blood-sucking flies (Jackson, 1989).

The degree of efficacy naturally depends on the interval between treatment and host defaecation or between treatment and insect feeding. For 9 days after the treatment of cattle at 0.2 mg/kg b.w. s.c., the faeces of the treated cattle completely failed to support the development of face-fly larvae, *Musca autumnalis* DeGeer, and for a further 5 days, the propagation of the fly was greatly reduced through abnormal pupation and diminished maturation of the adult (Meyer *et al.*, 1981). For 4 weeks after treatment with a similar injection, the faeces of treated cattle failed to support the development of horn fly larvae, *Haematobia irritans* (L.), (Miller *et al.*, 1981).

Concern has been expressed over the effects that this persistence of ivermectin may have on the dung inhabiting fauna as a whole, and the effect that this might have on the environment in terms of pollution (McCracken, 1987).

Schmidt (1983), working in the USA, investigated the possibility that ivermectin treatment of cattle could lead to accumulations of manure, and hence fouling of pastures. He treated cattle with an intramuscular injection of 0.2 mg/kg b.w. ivermectin, and, at the end of his experiments, concluded that the manure from treated animals appeared to disintegrate physically at the same rate as that from untreated animals. However, he also found a great reduction in the emergence of several endemic, non-target, insects from the manure of treated animals as compared to that from untreated animals e.g. the number of Sphaeroceridae and Sepsidae flies emerging was reduced by 97%.

In Britain, Wall & Strong (1987) reported that the faeces of calves carrying ruminal boluses, delivering ivermectin at 0.04 mg/kg b.w./day, failed to degrade in the normal way, and that this failure was associated with the absence of dung-degrading insects. Dung from untreated calves contained a characteristic dung-degrading invertebrate community, and, as a result, was well decayed 40 days after deposition and had largely disappeared by 100 days. In contrast, even after 100 days, dung from treated animals was remained largely intact, retained a solid crust, and showed signs of erosion only at the margins. Dung samples taken over the experimental period indicated that ivermectin delivered in this way, and excreted in the faeces of treated animals, had an insecticidal effect on the entire dung-degrading community, with the exception of earthworms which appeared to be unaffected by the chemical.

In Australia, Ridsdill-Smith (1988a & b) found that treatment of cattle with avermectin B_1, at the recommended dose rate of 0.2 mg/kg b.w. s.c., adversely affected the survival of the bushfly, *Musca vetustissima* Walker, and breeding of the introduced dung beetle, *Onthophagus binodis* Thurnberg, in the dung collected from treated cattle. No bush flies survived from egg to adult in dung collected from animals treated with avermectin B_1 2 weeks earlier, and survival did not return to normal until 8 weeks after treatment. Adult survival of *O. binodis* was not affected in dung of cattle treated with avermectin B_1, but oviposition was reduced and immature survival was zero in dung from animals treated 1 week previously, and did not return to normal until 8 weeks after treatment. To avoid harmful effects on dung beetles introduced to southwestern Australia, he recommended that cattle should not be treated with avermectin B_1 during spring, the main breeding period for many species of dung beetle in this area.

Similar results were obtained in Spain by Wardhaugh & Rodriguez-Menendez (1988) investigating the effects of ivermectin in dung on the development and survival of the dung-breeding fly *Orthelia cornicina* (F.), and the scarabaeine dung beetles *Copris hispanus* L., *Bubas bubalus* (Oliver) and *Onitis belial* F., e.g. dung collected from calves treated with a single injection of ivermectin, at 0.2 mg/kg b.w. s.c., was toxic to larvae of *O. cornicina* for up to 32 post-treatment. Their results also suggested that adult dung beetles may be susceptible to ivermectin poisoning when physiologically young.

Most recently, Madsen *et al.* (1990) in Denmark studied the effects of a single injection of ivermectin administered to cattle at 0.2 mg/kg b.w. s.c., under field and laboratory conditions. They found that faecally excreted ivermectin inhibited the development of larvae of dung-dwelling Diptera Cyclorrhapha in dung collected from cattle 0-30 days after treatment, and that dung beetle, *Aphodius* spp., and Diptera Nematocera larvae were inhibited in dung from animals treated 1 and 1-10 days previously, respectively. Excreted ivermectin remained active against a laboratory strain of the housefly, *Musca domestica* (L.), in dung pats exposed for 2 months in the field. They also discovered that the decomposition of faeces from cattle, treated up to 20 days previously, was delayed significantly when compared with untreated controls, and they ascribed this to the adverse effects of ivermectin residues on the primary dipteran decomposing fauna.

The only figure available (in the public domain) concerning the amount of ivermectin present in dung pats produced by cattle after treatment with ivermectin, is that provided by Jackson (1989) when, referring to unpublished data, she states that '..the estimated maximum concentration of ivermectin in faeces produced by cattle treated with the recommended, single, 200 mcg/kg b.w. s.c. dose is 0.353 ppm, during the first week after dosing'.

McCracken (1987) and Campbell (1989) should be consulted for additional information on the subject of ivermectin.

(e) Multivariate analysis methods used in this study

Multivariate analysis is the branch of mathematics that deals with the examination of numerous variables simultaneously: the need for multivariate analysis arises whenever more than one characteristic is measured on a number of individuals, and relationships among characters make it necessary for them to be studied simultaneously. The purpose of multivariate analysis is to treat multivariate data as a whole, summarizing the data and revealing their structure (Gauch, 1982).

A glossary of some of the terms commonly used in community ecology is given below (after Ter Braak, 1987):

Environmental variable - an explanatory variable of prime interest in the analysis.

Ordination axis - a theoretical explanatory variable, also termed a gradient.

Eigenvalue - a measurement of the importance of an ordination axis.

Species score - a value representing the location of a species along an ordination axis.

Sample score - a value for the location of a sample along an ordination axis.

Ordination diagram	- a scatter plot of the sample and/or species scores along one or more ordination axes.
Bi-plot	- an ordination diagram of two kinds of entities, e.g. species and environmental variables.

In community ecology, the customary input data are species abundances in a two-way samples-by-species data matrix, and there are three basic multivariate analysis strategies (Gauch, 1982):

(1) direct gradient analysis - used to study the distribution of species along recognized, easily measured, environmental gradients;

(2) ordination - which endeavours to represent sample and species relationships in a low-dimensional space;

(3) classification - which is the assignment of samples or species into classes or groups.

In (2) and (3), environmental interpretation is normally performed in a subsequent, independent step, and hence these methods are referred to as indirect gradient analysis techniques.

Gauch (1982) concluded that two complementary multivariate analysis methods, Detrended Correspondence Analysis (DECORANA: Hill, 1979b), a divisive ordination method based on reciprocal averaging, and Two-Way Indicator Species Analysis (TWINSPAN: Hill, 1979a), a polythetic divisive classification technique, were by far the best techniques available for analysing complex sample-by-species data arrays. The great value of these techniques is that a large array of species and samples, with large numbers of zero values, can be dealt with in an objective way independent of any prior knowledge about the samples other than the species present (Foster *et al.*, 1990).

Ordination by DECORANA

Ordination is the arrangement of species and samples in a low-dimensional space. The end product is a graph, usually two-dimensional, in which similar samples or species or both are close to each other and dissimilar entities are far apart (Gauch, 1982). The axes of this graph can be related to known environmental parameters, which may then be used to describe either sample characteristics of importance to the community structure, or the preferred environments of the species present (Luff *et al.*, 1989)

DECORANA (Hill, 1979b) performs ordinations on data by detrended correspondence analysis, a technique derived from a simpler method of ordination known as reciprocal averaging (Hill, 1973).

The most conspicuous fault of reciprocal averaging is the tendency for the second axis (and sometimes higher axes) to be strongly related to the first axis - a feature known as the arch effect. Detrended correspondence analysis avoids this arch effect by demanding not merely that there should be no correlation, but rather that there shall be no systematic relationship of any kind between the higher axes and the first (Hill, 1979b).

In addition to the arch effect, reciprocal averaging has another fault, i.e. the scaling of the axes does not have any clearly defined meaning. To counter this, detrended correspondence analysis incorporates a feature for rescaling the axes. This results in species turnover occurring at a uniform rate along the species ordination axis, and, consequently, results in equal distances in the ordination corresponding to equal differences in species composition (Hill, 1979b).

DECORANA also incorporates a 'downweighting' procedure, which allows, if desired, the influence of rare species in the data on the ordination of the samples to be minimized.

Classification by TWINSPAN

Polythetic divisive classification techniques use information on all the species in a data set. They begin with all the samples together in single cluster and successively divide the samples into smaller clusters, until, finally, each cluster contains only one sample or a specified small number of samples.

Hierarchical classification puts similar samples, or species, into groups, and, additionally, arranges the groups into a hierarchical, treelike structure (a dendrogram), which indicates relationships among the groups (Gauch, 1982).

TWINSPAN is derived from reciprocal averaging ordination and a form of iterative character weighting of the species in the data set (Hill, 1979a).

(1) The data are first ordinated by reciprocal averaging, and then the samples are initially divided into two clusters by breaking the ordination near its middle. Differential species are identified which are preferential to one side or other of this crude dichotomy (a species is regarded as differential if it occurs in at least 20% of the samples on one side of the dichotomy, and is at least twice as likely to occur on that side than on the other).

(2) A refined ordination is then carried out on the data, using only the differential species as a basis, and two clusters of samples are finally formed by division of this refined ordination.

(3) This process is then repeated on the two sample

subsets to give four clusters, and so on. In the present study, the divisive process of TWINSPAN was continued until (a) replicate samples were about to be separated (a process for which the term 'site integrity' has been coined), or (b) each further division produced two end-groups which were not ecologically distinct.

(4) TWINSPAN also carries out a simplified ordination, the 'indicator' ordination, on the data, based on only a few of the most highly differential species, i.e. species that only occur on one side of the division. If the dichotomy suggested by the refined ordination can be reproduced by division of the indicator ordination, then a set of indicator species is produced for each stage in the division process (these are the highly differential species used in the indicator ordination). If, on the other hand, (a) the two dichotomies from the refined and the indicator ordinations do not match up, or (b) there are no species which occur only on one side of the division or the other, then no indicator species are identified for each stage in the division process, and the dichotomy produced by TWINSPAN therefore represents the refined ordination of the data using all the differential species.

(5) After the sample classification, a corresponding species classification is produced, and the sample and species hierarchical classifications are used together to produce an arranged data matrix. This arranged data matrix is in the form of an ordered two-way table in which the correlation between sites and species occurrences is maximized. This, in effect, orders the sites and species so that the occurrences as nearly as possible occupy the leading diagonal, ordering both in such a way that the changes in species composition across the range of sites are readily identified.

One disadvantage of TWINSPAN is that it can only classify species presence/absence data. However, the 'pseudo-species' function in TWINSPAN can be used to take into account the quantitative aspect of a data set. This reduces the quantitative data to presence/absence data, without undue loss of information, by converting the abundance data into classes. Each class is treated thereafter as if it were a species in its own right, hence the name 'pseudo-species'. Therefore, if species abundances in a data set were converted into classes corresponding to 1-4, 5-9, 10-24 or >24 individuals, then, as these classes are non-exclusive, a sample in which e.g. 20 *Any species* adults occurred, would be registered as containing classes 1, 2 and 3 of *Any species* adults.

Direct gradient analysis by CANOCO

Recently, Ter Braak (1986 & 1987) developed a new multivariate method for direct gradient analysis, which is an extension of the indirect gradient analysis technique of detrended correspondence analysis. Canonical correspondence analysis (CANOCO) combines both species and environmental data in a DECORANA ordination, and is designed to detect the patterns of variation in the species data that can be explained 'best' by the observed environmental variables.

CANOCO produces a bi-plot which shows the distribution of sites and/or species in two ordination axes together with arrows representing the environmental variable. The relative lengths of the arrows indicate the amount of variation explained by each environmental variable (Eyre *et al.*, 1989).

Although the above methods were primarily developed for use in vegetation analysis, in recent years a number of authors have used them successfully in invertebrate studies, e.g. Wright *et al.* (1984); Eyre *et al.* (1986);

Luff *et al.* (1989).

It should be borne in mind that vegetation and invertebrate communities differ markedly e.g. with regard to ease of sampling. The vegetation at a site is relatively easy to sample (being stable in occurrence, and normally present in a recognizable form throughout most of the year), whereas it is much more difficult to sample invertebrates accurately (as they are mobile, with recognizable forms present for only part of the year). It is therefore perfectly feasible that the dominant species of invertebrate at a site could go undetected (e.g. through sampling at the wrong time of year), and so it is important that the results obtained from multivariate analysis of invertebrate data are considered carefully, before any firm conclusions are drawn.

Software

The data sets obtained from the present study were all analysed using microcomputer, rather than mainframe, versions of the above multivariate analysis techniques. TWINSPAN and DECORANA programmes were as provided by Carleton (1985), and CANOCO (version 2.1) as by Ter Braak (1987).

The microcomputer versions differ slightly in the format of their output, but otherwise would appear to to be compatible to the mainframe programmes, e.g. microcomputer and mainframe TWINSPAN analysis of the dung data set in Chapter 8 produced identical results.

CHAPTER THREE:
SAMPLING METHODOLOGY AND SAMPLE SITES ON ISLAY

INTRODUCTION

As the chough exhibits a marked preference for the north-western region of Islay throughout the year (Warnes, 1982; Bignal *et al.*, 1988), most fieldwork was conducted in that area. Four main sites were chosen for study - Ardnave, Coille, Coul and Sanaigmore (Fig. 3.1). The invertebrate fauna at each of the study sites was assessed by continuous pitfall trapping and by sampling soil and cow dung during each visit to the island. In all, 15 trips (each about 5 days long) were made between January 1988 and November 1989.

METHODS

Each pitfall trap consisted of a plastic cup (74 mm in diameter and 105 mm deep) set with its rim flush with the soil surface. A small quantity of ethylene glycol, a proprietary antifreeze solution, was put in each cup to act as a killing agent and preservative.

Between January 1988 and April 1989 a set of three such traps was positioned (in the form of a triangle with sides 1 m long) at each site under investigation. These traps were replaced at each site in April 1989 by bi-replicate sets of nine traps placed 20 m apart (each set forming a straight line with 2.5 m between traps). Each of the replacement traps had a covering of 2 cm chicken wire to prevent entry by small mammals. The traps were emptied and replenished with preservative during each trip to the island. Catches from the traps in each set were pooled at each collection and stored in 70% alcohol prior to identification.

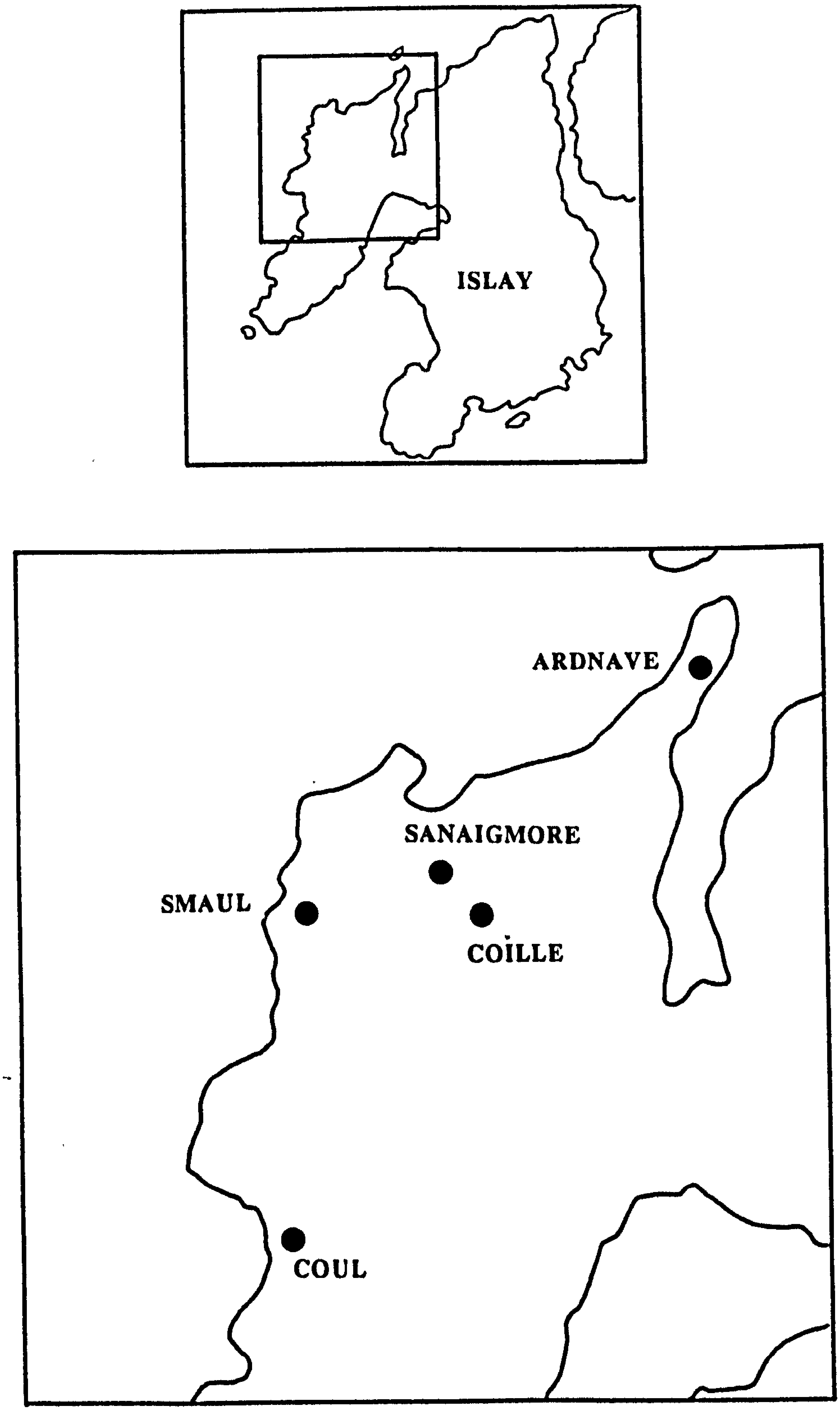


Fig. 3.1. Location of the sample sites on Islay

Soil was sampled by taking 20 soil cores (each 6.5 cm in diameter and 10 cm deep) from each site every visit. The cores were hand-sorted on the island, and the invertebrates extracted from each set of 20 were pooled and stored in 70% alcohol for later identification.

Cow dung of different ages was sampled at each site by taking two cores (dimensions as above) through each cow pat and into the soil beneath. The dung samples were transported to the College where the invertebrates were heat-extracted, pooled for each pat and stored in alcohol for subsequent identification.

Nomenclature throughout the study follows Kloet and Hincks (1964; 1976; 1977; 1978) except where recent revisions are available, e.g. Jessop (1986).

SAMPLE SITES

A description of each of the sample sites is given below:

Ardnave: an area of coastal pasture heavily grazed by sheep and cattle throughout the year. The set of three pitfall traps was placed in an area of sand grassland about 15 m above sea level (national grid ref. NR 290730). Until April 1989, two sets of soil cores were taken from this site on each visit - one from the area around the pitfall traps and another from a wet slope (NR 288735) where lapwing and oystercatcher were seen to feed. In April 1989 the bi-replicate sets of traps were placed in a similar area of grassland (NR 290739) about 1 km from the original trapping area. Only one set of soil samples, from the area around these traps, was taken on each subsequent visit to this site.

Sanaigmore: a rushy field, over a clayey soil, lying east of the road to the farm of that name. At the start of the study, the field was open to the surrounding moorland and sheep and cattle were free to graze throughout the year. In addition, cattle were provided with winter feed in this field during the first quarter of 1988.

The set of three pitfall traps was placed in one half of this field (NR 235698), at a height of about 20 m above sea level. A set of soil cores was taken from around the traps during each visit, and cow dung was sampled from the whole of the field when available. In March 1989 the field was fenced, and therafter only sheep grazed it. The bi-replicate sets of traps were positioned on the original trapping site in April 1989.

In the summer of 1989 it was intended to spread manure on one half of the field, and to investigate any subsequent effect on the invertebrate population. Bi-replicate sets of pitfall traps were therefore placed in the southern half of the field (NR 235 697) in July 1989, and an additional set of soil samples was taken from around these traps on each visit to the site. This was done to check that the invertebrate fauna of both areas of the field were similar before the manure was applied. Wet weather in August (see data below) prevented machinery access to the field at the beginning of September, and as a result the manure was never spread. However, the additional sets of traps were left in place, and provided data until the end of the study period.

Coille: an area of heather moorland, on peat, about 50 m above sea level. The set of three pitfall traps, and the bi-replicate replacements, were placed in the midst of the heather (NR 244686). Soil samples were taken from the area around the traps until March 1989. No soil samples were taken from this site after this date, as it was felt that there was too little return (in terms of invertebrates extracted from the soil cores) to justify the time and effort involved.

Cattle and sheep had access to this area throughout the year. The majority of the cow dung samples, however, were taken from an area of grassland pasture just off the moorland (at about 30 m above sea level). The cattle spent a large part of their time on this pasture, and, as a result, their dung was more plentiful and much easier found there than upon the moorland.

Coul: an area of coastal grassland grazed by sheep and cattle for most of the study period (in 1988 and 1989 the cattle were removed during the summer because the dry weather retarded grass growth). Pitfall traps placed between January - April 1988 in this area were lost, and so no data are available for that period. In April 1988 another set of three traps was placed in an area of sand grassland (NR 207639), at about 15 m above sea level. In April 1989 the bi-replicate sets of traps were placed in an area of similar grassland (NR 208635), about 1 km from the original trapping area. Soil samples were taken from the area around the traps during each visit. Cow dung was sampled, when available, from the surrounding area of sand grassland.

Smaul: an area of rushy coastal pasture, at the edge of heather moorland, grazed by sheep throughout the year. In 1989 there were plans to fence off part of this pasture for use as a hay field. Bi-replicate sets of pitfall traps were therefore placed in this pasture (NR 212685) in April 1989, and soil samples were taken from around the traps each visit. The intention was to monitor any change in the invertebrate population once grazing was discontinued and the herbage allowed to increase in length. The pasture had, however, not been fenced by July 1989 and so sampling at this site was discontinued.

CLIMATE AND WEATHER DATA

The climate of the Inner Hebrides (of which Islay is the southern most island) is maritime, with relatively low summer temperatures and high winter temperatures, frosts occurring at the lower elevations only occasionally. Radiation levels are high, especially along westward-facing coasts, where cloud amounts are lower. The low summer, and daytime, temperatures lead to a low evaporation demand, which, combined with moderate to high rainfall, results in soils which are very often saturated even in summer. The Hebrides share with Shetland and the Faroes the distinction of having the most maritime climate in Europe (Green & Harding, 1983).

No meteorological stations were in continuous operation on Islay during the period of study, and so data from the island of Colonsay (about 20 km north of Islay) were used. Colonsay and the north-western area of Islay are very similar in that both are low-lying areas exposed to the westerly wind belt. It was therefore felt that data from Colonsay would adequately reflect the weather conditions occurring at the sample sites.

The monthly daily mean air temperature is calculated as the mean of the monthly mean maximum + monthly mean minimum air temperatures for a month. Fig. 3.2 shows the monthly daily mean air temperatures (^{o}C) on Colonsay during 1988 and 1989. The long-term average is also shown. Both sets of figures closely resemble each other for the majority of these two years. It should be noted though, that December 1988 and January 1989 were 2.4 and 3.1 ^{o}C warmer than average, respectively. Also, at no time did the monthly daily mean air temperature fall below 4 ^{o}C.

The monthly total rainfall measurements (mm) on Colonsay during 1988 and 1989 are shown in Fig. 3.3, along with the long-term average. Although the actual figures varied somewhat, it can be seen that in 1988 the general trend was followed e.g. with April, May and June being the driest months. 1989, however, was more unusual, with February, March, August and October being considerably wetter, and November and December considerably drier, than average.

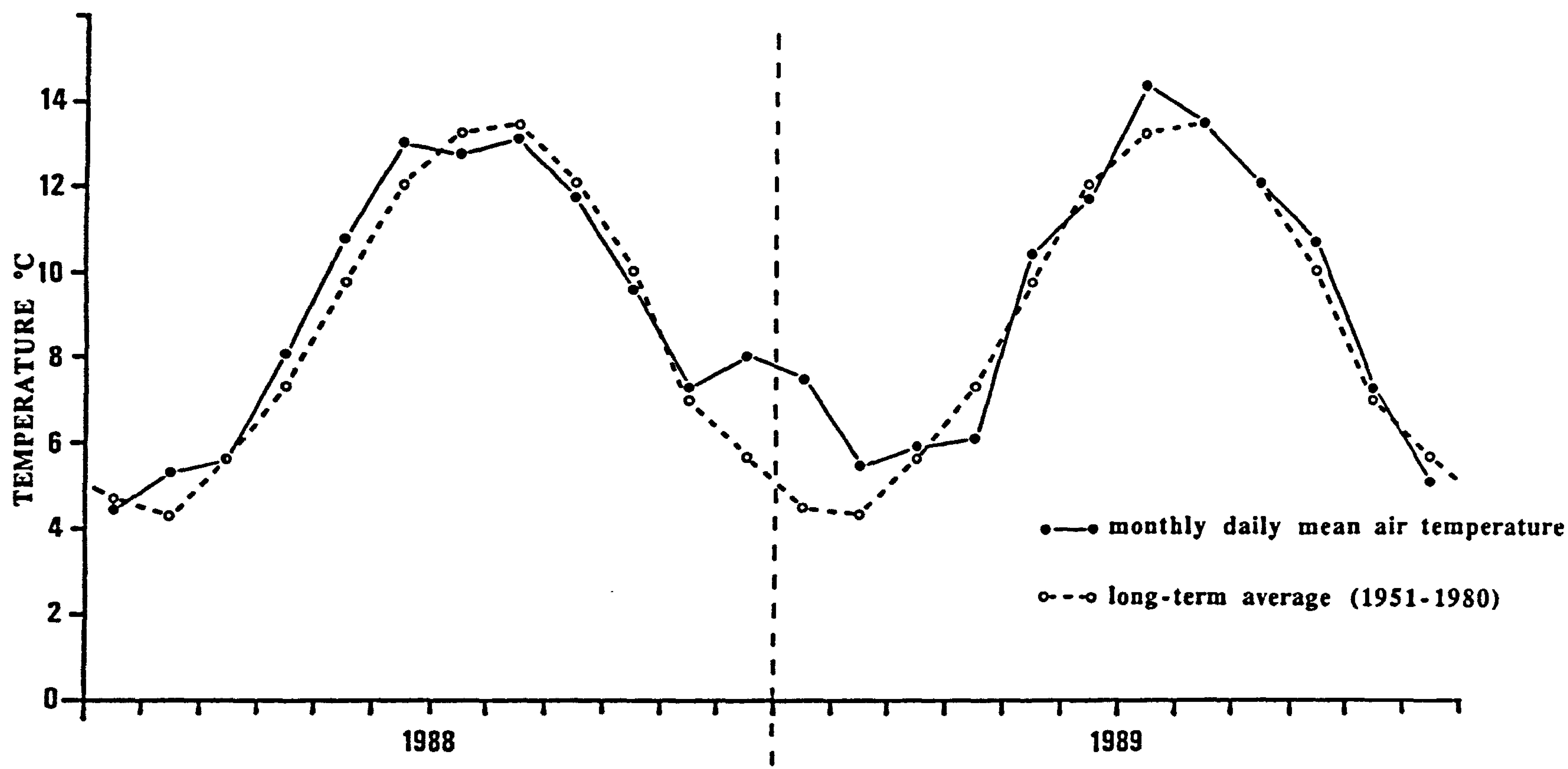


Fig. 3.2. Monthly daily mean air temperature (°C) on Colonsay during 1988 and 1989. Data from Meteorological Office (1988; 1989)

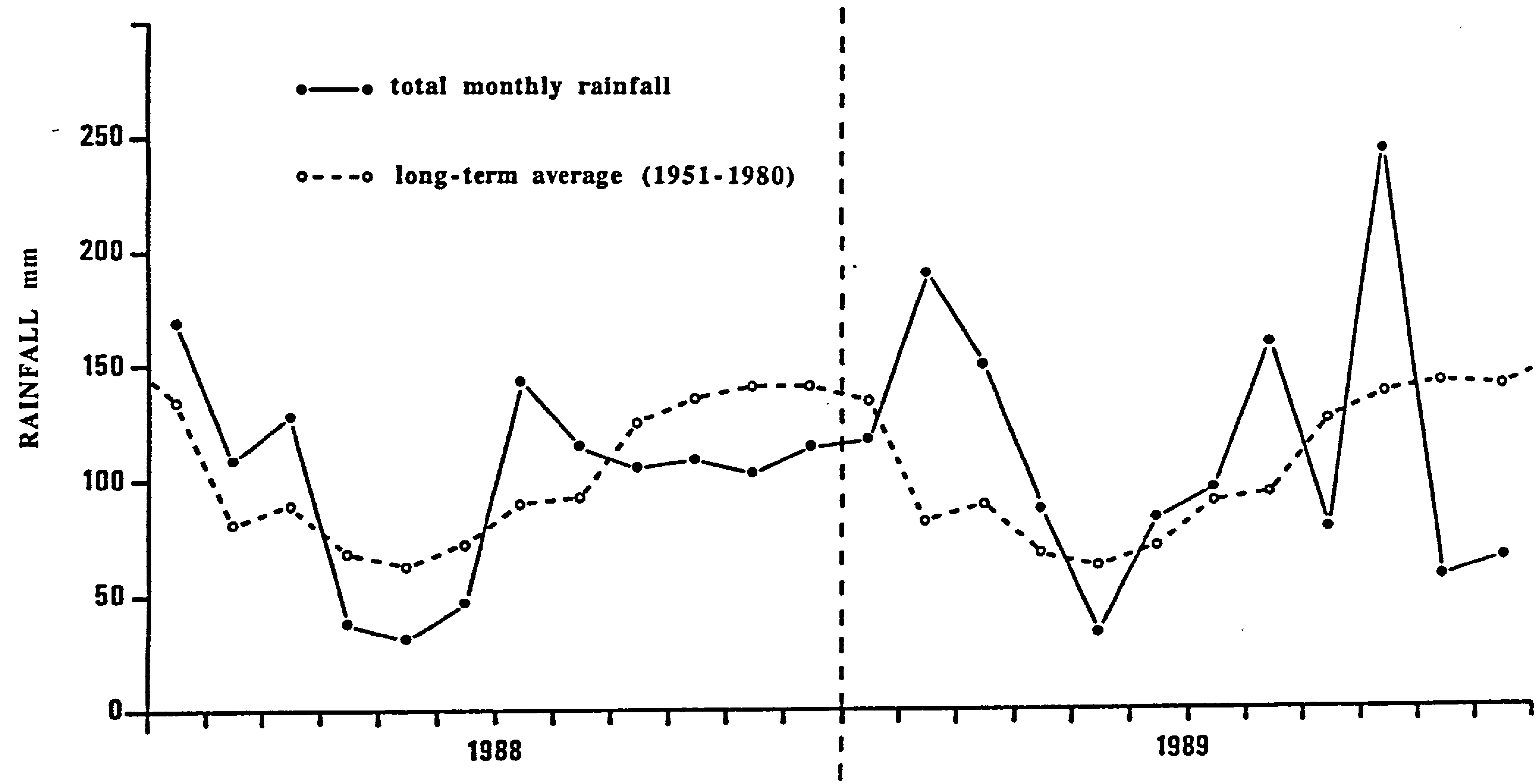


Fig. 3.3. Total monthly rainfall (mm) on Colonsay during 1988 and 1989. Data from Meteorological Office (1988; 1989)

CHAPTER FOUR:
ANALYSIS OF ISLAY PITFALL TRAP DATA

INTRODUCTION

Bignal *et al.* (1988) carried out a systematic sample survey of 1x1 km squares on Islay and used the data to classify the natural vegetation and other landscape features into standard types. On the basis of these results, all of Islay's 1x1 km squares were classified into eight Land Types.

Bird surveys were also carried out, and maps of nesting distribution, and of sightings during the summer and winter, were produced for all species of Annex 1 (EC Birds Directive) birds found on Islay. It then proved possible to look at the relationships between vegetation-types, land-types and these birds during summer and winter.

Choughs use a wide-range of land-types over the island. The birds show preference for rocky coasts and cliffs, farmland, and coastal pasture in both summer and winter. Sandy coast is not used preferentially during the summer, but does feature during the winter. During both periods, the majority of chough sightings were therefore of birds in some form of grassland vegetation, with moorland shrub vegetation also being selected (Bignal *et al.*, 1988; Curtis *et al.*, 1988).

Choughs probe for their food and also take surface prey items, exploiting seasonal abundances of certain invertebrates (Bullock, 1980; Warnes, 1982). The aims of the present study were to provide baseline data on the phenology of potential foods of the chough, and to provide a greater understanding of the factors affecting the distribution of these invertebrate populations.

The areas selected for study have been described in the previous chapter. The data obtained from pitfall trapping is analysed below, and analyses of data obtained from soil and cow dung sampling are dealt with in Chapters 5 and 6, respectively.

METHODS

Data collection

The pitfall trapping methodology is described for each site in Chapter 3. Each period over which invertebrates accumulated in the traps (hereafter referred to as a subsample) at each site is shown in Table 4.1.

Taxa were identified using standard keys (e.g Bolton & Collingwood, 1975; Brindle, 1977; van Emden, 1942; Hansen, 1987; Jessop, 1986; Joy, 1932; Lindroth, 1974; Peterson, 1977; Tottenham, 1954; Unwin, 1984). A total of 62 taxa were identified (Table 4.2). The number of each taxon present in each subsample was calculated, and, to allow comparison between all sets of pitfall traps, the numbers caught in the sets consisting of three traps were increased by a factor of 3.

Two data sets were used in the analyses - one containing taxa presence/absence, and the other taxa abundances (Appendix 1). These final data sets therefore contained information on 62 taxa from 74 subsamples.

Classification and ordination

(a) Presence/absence data:

The 74 subsamples were classified using TWINSPAN (see Chapter 2). Taxa and subsamples were ordinated in two axes using DECORANA (see Chapter 2) with all taxa being considered equally i.e. without downweighting of rare taxa.

TABLE 4.1. Sites on Islay, with associated subsamples, from which pitfall trap data was obtained. See text for further information

SITE	SUBSAMPLES (+ DATES BETWEEN COLLECTION)			
ARDNAVE	AA01 (1801-230388)	AA02 (2303-280488)	AA03 (2804-090688)	AA04 (0906-150788)
	AA05 (1507-111088)	AA06 (1110-301188)	AA07 (3011-170189)	AA08 (1701-070389)
	AA09 (0703-260489)			
	AB01 (2604-030689)	AB02 (2604-030689)	AB03 (0306-180789)	AB04 (0306-180789)
	AB05 (1807-120989)	AB06 (1807-120989)	AB07 (1209-091189)	AB08 (1209-091189)
COILLE	BB01 (1501-220388)	BB02 (2203-280488)	BB03 (2804-110688)	BB04 (1106-140788)
	BB05 (1407-121088)	BB06 (1210-011288)	BB07 (0112-180189)	BB08 (1801-100389)
	BB09 (1003-270489)			
	BB10 (2704-040689)	BB11 (2704-040689)	BB12 (0406-180789)	BB13 (0406-180789)
	BB14 (1807-130989)	BB15 (1807-130989)	BB16 (1309-071189)	BB16 (1309-071189)
COUL	CA01 (2904-080688)	CA02 (0806-130788)	CA03 (1307-101088)	CA04 (1010-291188)
	CA05 (2911-180189)	CA06 (1801-090389)	CA07 (0903-250489)	
	CB01 (2504-020689)	CB02 (2504-020689)	CB03 (0206-170789)	CB04 (0206-170789)
	CB05 (1707-110989)	CB06 (1707-110989)	CB07 (1109-081189)	CB08 (1109-081189)
SANAIGMORE	SA01 (1801-210388)	SA02 (2103-280488)	SA03 (2804-100688)	SA04 (1006-130788)
	SA05 (1307-121088)	SA06 (1210-291188)	SA07 (2911-180189)	SA08 (1801-090389)
	SA09 (0903-270489)			
	SA10 (2704-040689)	SA11 (2704-040689)	SA12 (0406-190789)	SA13 (0406-190789)
	SA14 (1907-120989)	SA15 (1907-120989)	SA16 (1209-071189)	SA17 (1209-071189)
	SB01 (1907-120989)	SB02 (1907-120989)	SB03 (1209-071189)	SB04 (1209-071189)
SMAUL	SM01 (2804-020689)	SM02 (2804-020689)	SM03 (0206-190789)	SM04 (0206-190789)

TABLE 4.2. Taxa identified in the pitfall traps on Islay. An abbreviation (7-8 letters) and a code number are shown for each taxon.

COLEOPTERA

CANTHARIDAE

Cantharidae larvae	CANTLARV	15
Rhagonycha femoralis (Brullé) adults	RHAGFEMO	50

CARABIDAE

Amara spp. adults	AMARASPP	4
Calathus fuscipes (Goeze) adults	CALAFUSC	13
C. melanocephalus (L.) adults	CALAMELA	14
Carabus arvensis Herbst adults	CARAARVE	16
C. glabratus Paykull adults	CARABLAB	17
C. granulatus L. adults	CARAGRAN	18
Carabidae larvae	CARALARV	19
C. violaceus L. adults	CARAVIOL	20
Dyschirius spp. adults	DYSCHSPP	24
Loricera pilicornis (Fab.) adults	LORIPILI	32
Nebria brevicollis (Fab.) adults	NEBRBREV	36
Notiophilus spp. adults	NOTIOSPP	37
Pterostichus madidus (Fab.) adults	PTERMADI	42
P. niger (Schaller) adults	PTERNIGE	43
P. nigrita (Paykull) adults	PTERNIGR	44
P. strenuus (Panzer) adults	PTERSTRE	45
P. versicolor (Sturm) adults	PTERVERS	46
Synuchus nivalis (Panzer) adults	SYNUNIVA	58
Trechus spp. adults	TRECHSPP	60

CHRYSOMELIDAE

Halticinae adults	FLEABEET	29

COCCINELIDAE

Coccinela-11-punctata L. adults	COCCPUNC	22

CURCULIONIDAE

Alophus triguttatus (Fab.) adults	ALOPTRIT	3
Ceuthorrhynchidius troglodytes (Fab.) adults	CEUTTROG	21
Hypera spp. adults	HYPERSPP	28
Philopedon plagiatus (Schaller) adults	PHILPLAG	41
Sitona spp. adults	SITONSPP	28

ELATERIDAE

Agriotes obscurus (L.) adults	AGRIOBSC	1
Hypnoides riparius (Fab.) adults	HYPNRIPA	29
Denticollis linearis (L.) adults	DENTLINE	23

Table 4.2 cont:

HYDROPHILIDAE		
Megasternum obscurum (Marsham) adults	MEGAOBSC	33
LEIODIDAE		
Leiodidae adults	LEIOADUL	30
SCARABAEIDAE		
Aphodius ater (Degeer) adults	APHOATER	5
A. contaminatus (Herbst) adults	APHOCONT	6
A. depressus (Kugelann) adults	APHODEPR	7
A. fimetarius (L.) adults	APHOFIME	8
A. foetidus (Herbst) adults	APHOFOET	9
A. prodromus (Brahm) adults	APHOPROD	10
A. rufipes (L.) adults	APHORUFI	11
A. sphacelatus (Panzer) adults	APHOSPAC	12
Serica brunnea (L.) adults	SERIBRUN	51
STAPHYLINIDAE		
Aleocharinae adults	ALEOCHAR	2
Olophrum spp. adults	OLOPHSPP	38
Philonthus laminatus (Creutzer) adults	PHILLAMI	39
Philonthus spp. adults	PHILOSPP	40
Quedius spp. adults	QUEDISPP	47
Q. molochinus (Gravenhorst) adults	QUEDMOLO	48
Q. tristis (Gravenhorst) adults	QUEDTRIS	49
Staphylinus aenocephalus Degeer adults	STAPAENO	54
S. erythropterus L. adults	STAPERYT	55
Staphylinidae larvae	STAPLARV	56
Stenus spp. adults	STENUSPP	57
Tachyporinae adults	TACHYPOR	59
Xantholinus glabratus (Gravenhorst) adults	XANTGLAB	61
Xantholinus spp. adults	XANTHSPP	62
OTHER		
Araneae - Spiders	SPIDERS	53
Dermaptera - *Forficula auricularia* L.	FORFAURI	26
Diplopoda - Millipedes	MILIPEDE	34
Formicidae - *Myrmica ruginodis* Nylander	MYRMRUGI	35
Lepidopteran larvae	LEPILARV	31
Opiliones - Harvestmen	HARVEMEN	27

(b) Abundance data:

Taxa and subsamples were ordinated in three axes using DECORANA. All taxa were considered equally.

After analyses of both data sets, groups of subsamples were interpreted as representing distinct taxa assemblages. The ordination scores derived from DECORANA, measured in standard deviations of species 'turnover' (Hill, 1979b), were used to calculate (a) the mean score, for the first two axes, of each end-group interpreted from the presence/absence data, and (b) the centroid mean score, for the first three axes, of each end-group interpreted from the abundance data.

The distance of each subsample within an end-group from the end-group's mean score or centroid was then calculated. This typicalness measurement (terminology of Eyre *et al.*, 1986) is related to the probability of end-group membership, and was calculated in order to check the validity of the end-groups interpreted from the ordination plots.

Phenology

For each site, taxa that were considered potential chough prey items were extracted from the abundance data set, and their occurrences in the subsamples were plotted for the period that the traps were in position.

RESULTS

Classification and ordination

(a) Presence/absence data

The classification of the presence/absence data is given in Fig. 4.1(a), together with the indicator taxa at each

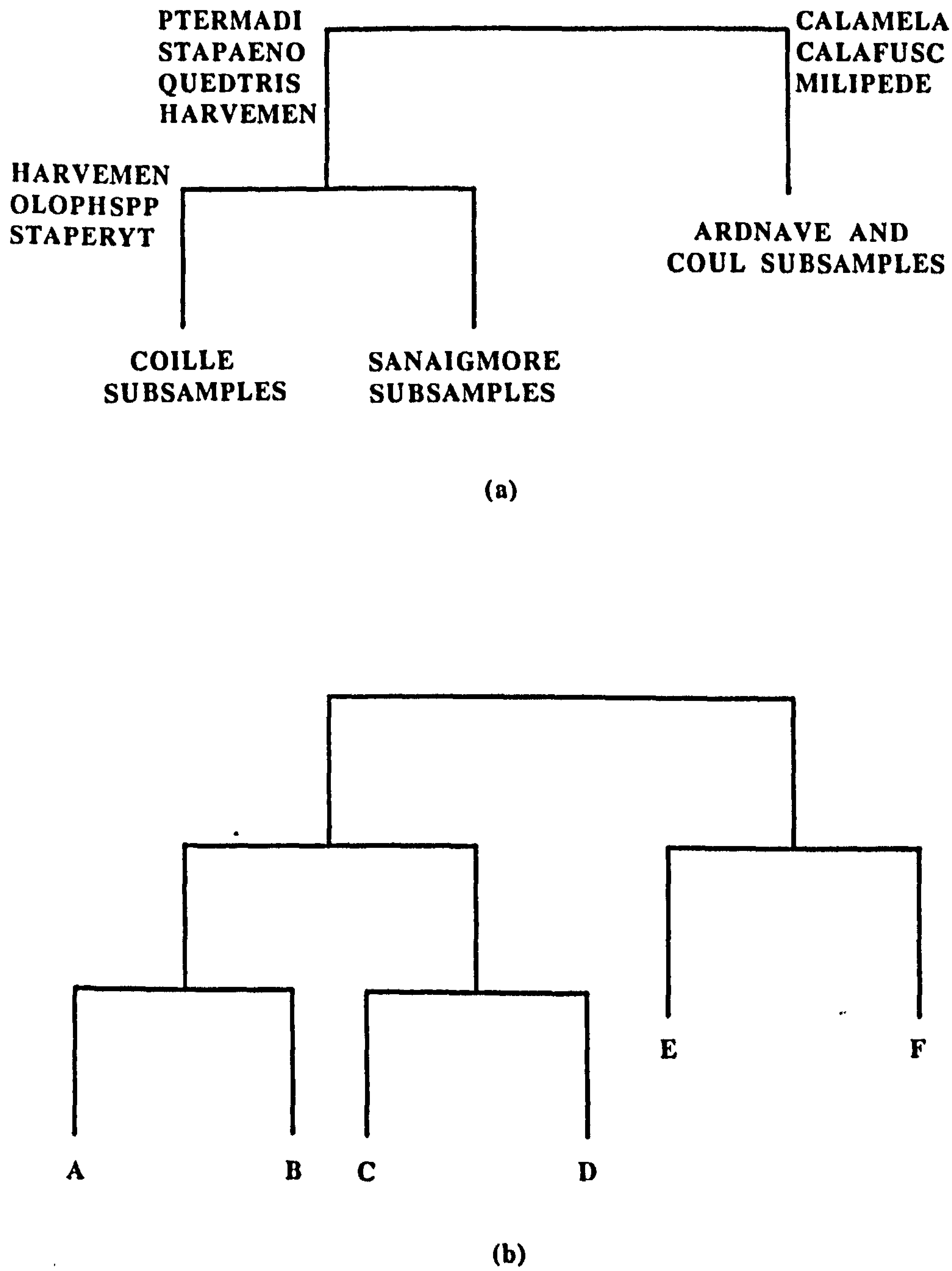


Fig. 4.1. Multivariate analysis of the pitfall trap data sets: (a) dendrogram showing the TWINSPAN classification of the presence/absence data. The indicator taxa at each division are shown (abbreviations as in Table 4.2); (b) the same, showing the proposed additional end-groups interpreted after DECORANA ordination of the data (Fig. 4.2).

division. The first division separates the Ardnave and Coul subsamples from those from Coille and Sanaigmore, and the second division separates the subsamples from the latter two sites. From ordination of the data (which is considered in detail later) it was evident that these groupings of subsamples could be separated further, as is proposed in Fig. 4.1(b).

Six end-groups were thereby recognized as representing distinct taxa assemblages. The subsamples within each end-group are shown in Table 4.3, and the frequency of occurrence of each taxon within these end-groups is given in Table 4.4(a). The mean number of taxa per subsample for each of the six end-groups are given in Table 4.5. The end-groups were described as follows:

End-group A: 'winter' subsamples from the heather moorland at Coille (collected January-March 1988; October 1988-April 1989). Taxa active during these periods were Carabidae larvae, *Olophrum* spp. adults and *Staphylinus aenocephalus* adults.

End-group B: 'summer' subsamples from Coille (March-October 1988; April-November 1989), containing a greater variety of taxa. *Nebria brevicollis, Pterostichus strenuus, Carabus arvensis, Quedius molochinus* and *Staphylinus erythropterus* adults were prevalent at these times, along with Staphylinidae larvae and *Myrmica ruginodis* ants.

End-group C: 'summer' subsamples from the old rushy pastures at Sanaigmore (April-October 1988; April-November 1989) and Smaul (April-July 1989). As in end-group B, a large number of taxa were prevalent at these times e.g. *Amara* spp., *Pterostichus madidus, P. strenuus, Philonthus* spp. and Tachyporinae adults, Staphylinidae larvae and *Myrmica ruginodis* ants.

TABLE 4.3. Multivariate analysis of the pitfall trap data sets: end-groups, with associated subsamples, interpreted from TWINSPAN and DECORANA analysis of the presence/absence data. See Table 4.1 and text for further information.

END-GROUP	SUBSAMPLES								
A	BB01	BB06	BB07	BB08	BB09				
B	BB02	BB03	BB04	BB05	BB10	BB11	BB12	BB13	BB14
	BB15	BB16	BB17						
C	SA03	SA04	SA05	SA10	SA11	SA12	SA13	SA14	SA15
	SA16	SA17	SB01	SB02	SB03	SB04	SM01	SM02	SM03
	SM04								
D	SA01	SA02	SA06	SA07	SA08	SA09			
E	AA05	AA06	AA07	AA08	AA09	CA05	CA06		
F	AA01	AA02	AA03	AA04	AB01	AB02	AB03	AB04	AB05
	AB06	AB07	AB08	CA01	CA02	CA03	CA04	CA07	CB01
	CB02	CB03	CB04	CB05	CB06	CB07	CB08		

TABLE 4.4. Multivariate analysis of the pitfall trap data sets: the frequency of occurrence of taxa within the end-groups derived (a) from TWINSPAN and DECORANA analysis of the presence/absence data set and (b) from DECORANA analysis of the abundance data set, where a taxon occurs in >20% of the subsamples in one of the end-groups (D=21-40%; C=41-60%; B=61-80%; A=81-100%). The taxa order is derived from the TWINSPAN analysis of the presence/absence data and the abbreviations are as shown in Table 4.2.

TAXA	(a) END-GROUP						(b) END-GROUP						
	A	B	C	D	E	F	A	B	C	D	E	F	G
CARAARVE	-	B	-	-	-	-	-	A	-	-	-	-	-
HARVEMEN	A	A	-	-	-	-	A	A	-	D	-	-	-
OLOPHSPP	A	C	-	-	-	-	A	C	-	-	-	-	-
CARAVIOL	-	C	-	-	-	-	D	D	-	-	-	-	-
QUEDMOLO	-	A	-	-	-	-	D	B	-	-	-	-	-
STAPERYT	D	A	D	-	-	-	D	A	-	-	-	-	-
CARAGLAB	-	D	-	-	-	-	-	D	-	-	-	-	-
CANTLARV	-	-	-	B	-	-	-	-	-	B	-	-	-
RHAGFEMO	-	-	D	-	-	-	-	-	-	-	-	-	-
SYNUNIVA	-	-	B	-	-	-	-	-	C	D	-	-	-
ALOPTRIT	-	-	D	-	-	-	-	-	D	-	-	-	-
PTERVERS	-	-	C	-	-	-	-	-	D	D	-	-	-
AGRIOBSC	-	D	C	-	-	-	-	D	C	-	-	-	-
HYPNRIPA	-	D	C	-	-	-	-	D	C	-	-	-	-
PTERNIGR	-	-	-	D	-	-	-	-	-	D	-	-	-

Table 4.4 cont:

TAXA	(a) END-GROUP A	B	C	D	E	F	(b) END-GROUP A	B	C	D	E	F	G
PTERMADI	-	C	B	-	-	-	D	B	C	D	?	-	-
PTERNIGE	-	C	C	-	-	-	-	C	D	D	-	-	-
QUEDTRIS	-	C	B	-	-	-	-	C	C	D	-	-	-
LEPILARV	-	D	B	-	-	-	-	D	C	-	-	-	-
MYRMRUGI	C	A	B	-	-	D	B	A	C	-	-	-	C
PTERSTRE	-	B	B	D	-	D	-	C	B	-	-	D	D
STAPAENO	A	B	B	A	-	D	A	B	A	D	-	-	C
LORIPILI	-	-	D	-	-	-	-	-	-	-	D	-	-
MEGAOBSC	-	D	C	B	-	D	-	D	C	A	-	C	D
APHODEPR	-	-	-	-	-	-	-	-	-	-	-	D	-
APHOSPAC	-	-	D	-	-	-	-	-	D	-	-	D	-
APHOATER	-	-	C	-	-	D	-	-	D	-	-	D	-
PHILLAMI	-	D	C	-	-	D	-	-	C	-	-	-	-
PHILOSPP	-	-	B	-	-	D	-	-	B	-	C	D	-
CARALARV	A	-	C	D	B	B	A	B	C	D	A	C	B
QUEDISPP	C	C	C	D	-	B	A	D	C	-	C	C	C
SITONSPP	-	-	B	-	-	C	-	-	B	-	C	C	C
AMARASPP	-	-	B	-	D	B	-	-	B	-	C	B	B
STENUSPP	-	D	D	-	-	D	-	D	D	D	-	D	D
XANTHSPP	-	-	B	C	D	C	-	-	C	A	C	D	B
NEBRBREV	C	A	C	-	B	C	B	A	C	-	C	B	C
SPIDERS	A	A	A	A	A	A	A	A	A	A	A	A	A
STAPLARV	C	B	A	B	A	B	A	C	A	A	A	B	B
TACHYPOR	C	D	A	A	C	B	D	D	A	A	A	A	C
APHOFOET	-	-	-	-	B	-	-	-	-	-	B	D	-
COCCPUNC	-	-	-	-	-	-	-	-	-	-	D	D	-
PHILPLAG	-	-	-	-	-	C	-	-	-	-	-	B	D
APHORUFI	-	-	-	-	-	D	-	-	-	-	D	-	-
LEIOADUL	-	-	D	-	C	D	-	-	-	-	-	B	-
ALEOCHAR	D	-	D	-	D	C	D	-	-	B	-	B	D
CALAFUSC	-	D	D	-	D	A	-	C	-	-	C	A	B
CALAMELA	-	C	-	-	D	A	-	B	-	-	C	A	A
NOTIOSPP	-	C	-	-	-	B	-	C	-	-	C	D	C
XANTGLAB	-	-	D	-	D	C	-	-	D	-	C	-	B
APHOCONT	-	-	-	-	-	D	-	-	-	-	C	-	-
FORFAURI	-	-	-	-	-	D	-	-	-	-	-	D	D
MILIPEDE	-	-	-	-	-	B	-	-	-	-	-	D	A
FLEABEET	-	-	-	-	-	D	-	-	-	-	-	D	C
SERIBRUN	-	-	-	-	-	D	-	-	-	-	-	-	D
CEUTTROG	-	-	-	-	-	-	-	-	-	-	-	-	D
DYSCHSPP	-	-	-	-	-	-	-	-	-	-	-	-	D
HYPERSPP	-	-	-	-	-	D	-	-	-	-	-	-	C
TRECHSPP	-	-	-	-	-	D	-	-	-	D	-	-	D

TABLE 4.5. Multivariate analysis of the pitfall trap data sets: number of subsamples, mean number of taxa per subsample (+ range) and mean typicalness measurements (+ range), in standard deviations of species turnover x 100 without downweighting of rare taxa, of the 6 end-groups interpreted from the TWINSPAN and DECORANA analysis of the presence/absence data set.

END-GROUP	NUMBER OF SUBSAMPLES	MEAN NUMBER OF TAXA (+RANGE)	MEAN TYPICALNESS MEASUREMENT (+RANGE)
A	5	10 (8-13)	25 (14-46)
B	12	18 (12-25)	23 (10-33)
C	19	20 (10-31)	29 (5-20)
D	6	8 (5-9)	26 (9-34)
E	7	8 (5-12)	32 (17-47)
F	25	18 (6-28)	38 (6-136)

End-group D: 'winter' subsamples from Sanaigmore (January-April 1988; October 1988-April 1989), containing far fewer taxa. Cantharidae larvae and *Staphylinus aenocephalus*, *Megasternum obscurum* and Tachyporinae adults were active at these times.

End-group E: subsamples from the sand grassland at Ardnave (July 1988-April 1989) and Coul (November 1988-March 1989) which could loosely be termed 'winter' subsamples. Taxa occurring in these subsamples included Carabidae and Staphylinidae larvae, and *Nebria brevicollis* and *Aphodius foetidus* adults.

End-group F: a composite group of Ardnave (January-July 1988; April-November 1989) and Coul (April-November 1988; March-November 1989) 'summer' subsamples. Prevalent taxa were *Calathus fuscipes*, *C. melanocephalus*, *Amara* spp., *Notiophilus* spp., *Quedius* spp. and Tachyporinae adults, Carabidae and Staphylinidae larvae, and millipedes.

Fig. 4.2 shows the axes 1 by 2 ordination plot, without downweighting of rare taxa, of the 74 subsamples used to classify end-groups. The mean subsample scores (and the associated standard errors) in each dimension are given for each end-group. The variance accounted for (based on eigenvalues of 0.357 and 0.155) was 70 and 30% for axes 1 and 2 respectively.

Axis 1 appears to be related to some feature of the soil, possibly moisture content, at each site, since the sand grassland sites (Ardnave and Coul) lie at one extreme, and the peat (Coille) and clay (Sanaigmore and Smaul) sites lie at the other.

Axis 2 appears to be related to seasonality, as the 'winter' subsamples (end-groups A, D and E) had the highest scores along the axis, whilst the 'summer' subsamples (end-groups B, C and F) had the lowest.

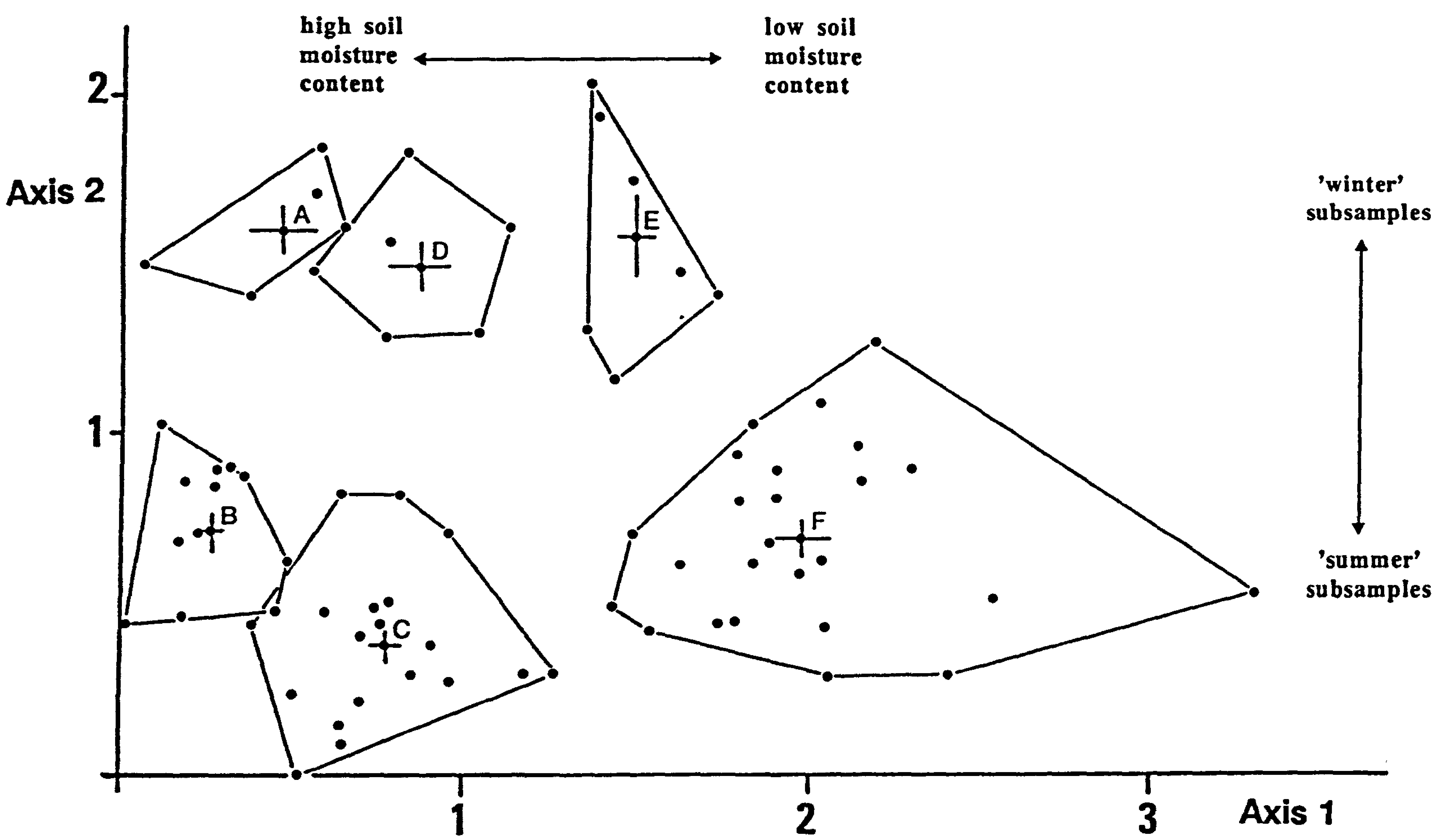


Fig. 4.2. Multivariate analysis of the pitfall trap data sets: axis 1 by axis 2 plot of the DECORANA ordination of the presence/absence data, without downweighting of rare taxa. Polygons enclose space containing all the subsamples in each end-group (A-F). Mean score and associated standard error in each dimension of the ordination are given for the six end-groups.

'Winter' and 'summer' subsamples from the sand grassland sites were present in end-group F, but did not separate well in axis 2. This would suggest that the taxa active during 'winter' and 'summer' at these sites did not differ as markedly as at the other sites.

The mean typicalness measurements for each of the six end-groups interpreted are given in Table 4.5. It can be seen that all these values are small. This, together with the fact that the standard errors of the mean subsample scores on each axis are also small (relative to the distance between mean subsample scores), would indicate that the end-groups interpreted from the analyses were valid.

(b) Abundance data

Seven end-groups were interpreted from the DECORANA analysis, without downweighting of rare taxa, as representing distinct taxa assemblages. The centroids of these end-groups are plotted against the first three DECORANA axes in Fig. 4.3, and their positions and relative distances from one another are given in table 4.7. The subsamples within each end-group are shown in Table 4.6, and the frequency of occurrence of each taxon within these end-groups is given in Table 4.4(b). The mean number of taxa per subsample for each of the end-groups are given in Table 4.8. The end-groups were described as follows:

End-group A: 'winter' subsamples from the heather moorland at Coille (collected January-March 1988; October 1988-March 1989; September-November 1989). Taxa active at these times included *Staphylinus aenocephalus*, *Quedius* spp. and *Olophrum* spp. adults, as well as Carabidae and Staphylinidae larvae.

End-group B: 'summer' subsamples from Coille (March-October

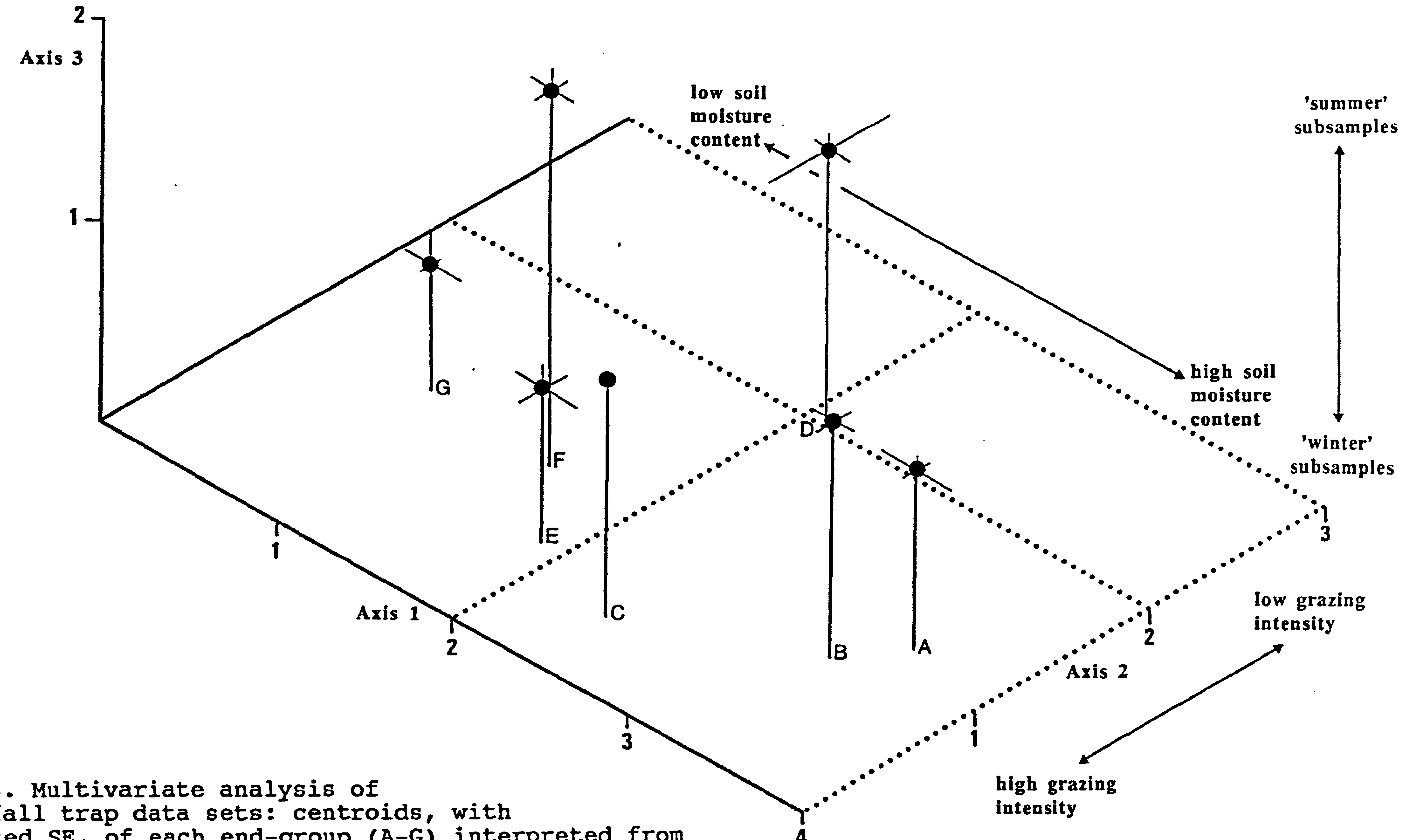


Fig. 4.3. Multivariate analysis of the pitfall trap data sets: centroids, with associated SE, of each end-group (A-G) interpreted from DECORANA analysis of the abundance data, without downweighting of rare taxa, plotted against the first three DECORANA axes.

TABLE 4.6. Multivariate analysis of the pitfall trap data sets: end-groups, with associated subsamples, interpreted from DECORANA analysis of the abundance data set. See Table 4.1 and text for further information.

END-GROUP	SUBSAMPLES							
A	BB01	BB06	BB07	BB08	BB16	BB17			
B	BB02	BB03	BB04	BB05	BB09	BB10	BB11	BB12	BB13
	BB14	BB15							
C	SA01	SA02	SA03	SA04	SA08	SA09	SA10	SA11	SA12
	SA13	SA14	SA15	SA16	SA17	SB01	SB02	SB03	SB04
	SM01	SM02	SM03	SM04					
D	SA05	SA06	SA07						
E	AA06	AA07	AA08	AB05	AB06	AB07	AB08		
F	AA01	AA02	AA03	AA04	AA05	AA09	AB01	AB02	AB03
	AB04								
G	CA01	CA02	CA03	CA04	CA05	CA06	CA07	CB01	CB02
	CB03	CB04	CB05	CB06	CB07	CB08			

TABLE 4.7. Multivariate analysis of the pitfall trap data sets: position, with associated SE, on each DECORANA axis and distances between centroids of each end-group interpreted from DECORANA analysis of the abundance data set. All positions and distances are in DECORANA axis units.

END-GROUP	POSITION			DISTANCE FROM END-GROUP					
	Axis: 1	2	3	B	C	D	E	F	G
A	350±20	112±6	94±6	45	130	166	169	221	270
B	331±12	83±8	122±2		95	163	149	193	256
C	246±3	40±5	122±4			160	72	131	185
D	215±10	196±35	142±6				151	125	178
E	190±18	60±14	81±11					122	118
F	151±12	100±10	190±8						142
G	82±18	105±5	66±18						

TABLE 4.8. Multivariate analysis of the pitfall trap data sets: number of subsamples, mean number of taxa per subsample (+ range) and mean typicalness measurements (+ range), in standard deviations of species turnover x 100 without downweighting of rare taxa, of the 7 end-groups interpreted from the DECORANA analysis of the abundance data set.

END-GROUP	NUMBER OF SUBSAMPLES	MEAN NUMBER OF TAXA (+RANGE)	MEAN TYPICALNESS MEASUREMENT (+RANGE)
A	6	12 (8-16)	44 (23-80)
B	11	18 (10-25)	42 (17-61)
C	22	18 (5-31)	30 (11-50)
D	3	10 (7-16)	49 (21-71)
E	7	12 (5-19)	58 (16-80)
F	10	16 (6-26)	48 (27-86)
G	15	17 (6-28)	81 (14-221)

1988; March-September 1989). *Staphylinus erythropterus*, *Carabus arvensis*, *Nebria brevicollis* and *Quedius molochinus* adults were prevalent, along with *Myrmica ruginodis* ants. A greater variety of taxa were present in this end-group compared to A.

End-group C: contained the majority of subsamples from the rushy pasture at Sanaigmore (January-July 1988; January-November 1989) and all the subsamples from the similar pasture at Smaul (April-July 1989). Taxa collected at these sites included Staphylinidae larvae and *Pterostichus strenuus*, *Staphylinus aenocephalus*, *Amara* spp., *Philonthus* spp. and Tachyporinae adults.

End-group D: contained the remaining subsamples from Sanaigmore (July 1988-January 1989). Cantharidae and Staphylinidae larvae, and *Megasternum obscurum*, Aleocharinae, and Tachyporinae adults, were prevalent in these 'autumn-winter' subsamples.

End-group E: 'winter' subsamples from the sand grassland at Ardnave (October 1988-March 1989; July-November 1989), containing Carabidae and Staphylinidae larvae, and *Aphodius foetidus* and Tachyporinae adults.

End-group F: 'summer' subsamples from Ardnave (January-October 1988; March-July 1989). *Calathus fuscipes*, *C. melanocephalus*, *Amara* spp., Tachyporinae and *Philopedon plagiatus* adults were among the taxa prevalent.

End-group G: all the subsamples from the area of sand grassland at Coul (April 1988-November 1989). A great variety of taxa were active at this site during this period, including *Calathus fuscipes*, *C. melanocephalus* and *Amara* spp. adults, millipedes, and Carabidae and Staphylinidae larvae.

The variance accounted for by each axis in Fig. 4.3 (based on eigenvalues of 0.677, 0.466 and 0.223) was 50, 33 and 17% for axes 1, 2 and 3 respectively.

As with the analysis of the presence absence data, axis 1 appears to be related to some feature of the soil, with peat soil at one extreme and sandy soil at the other.

Axis 2, however, would appear to be related to grazing intensity and the length of the grass, since end-group D lies at one extreme of this axis, and the remaining end-groups lie reasonably together at the other. The subsamples in end-group D correspond to a period when very little grazing occurred at this site, allowing the herbage to build up. Taxa prevalent in this end-group (*Megasternum obscurum*, Tachyporinae and Aleocharinae adults) were probably attracted by the resulting decomposing plant layer.

Axis 3 appears to be related to seasonality since the 'summer' subsamples had the highest scores along this axis, whilst the 'winter' subsamples had the lowest.

The mean typicalness measurements for each of the 7 end-groups are given in Table 4.8. All the measurements are reasonably low. Only in end-group G does a subsample occur with a very large value. Such large values may indicate that the subsample contains an assemblage not previously recognized in interpretation of the analysis (Eyre *et al.*, 1986). In this subsample large numbers of two taxa, *Calathus melanocephalus* and *Forficula auricularia*, occur (see phenology section). The large typicalness measurement would therefore appear to be due to the large abundances of these two taxa, and therefore not a result of any differences in the taxa present.

The calculated distances between end-groups (Table 4.7) are a measure of the similarity between end-groups as defined by the analysis. End-groups A and B were close, as were end-groups C and E. However, the standard errors of the mean site scores on each axis were reasonably small relative to the distances between centroids (Fig. 4.3), indicating that the definitions of the end-groups described were valid.

Phenology

Figs. 4.4 - 4.7 give an indication, for each of the main sites, of the seasonal activity of some of the frequently occuring taxa considered potential chough prey items:

Coille (Fig. 4.4): Carabidae larvae were most active between November and March, and the peak of activity of adults of the large carabid, *Carabus arvensis*, appeared to be related to the tailing off of this larval activity. Staphylinidae larvae were collected in low numbers in the traps over most of the study period. It is interesting to note that the two large staphylinids, *Staphylinus erythropterus* and *S. aenocephalus*, showed summer and winter peaks of activity, respectively. The ant *Myrmica ruginodis* was active on the moorland in low numbers during most of 1988, and reached a peak of activity during June and July 1989.

Sanaigmore (Fig. 4.5): *Staphylinus aenocephalus* adults again exhibited a winter peak of activity. Staphylinidae larvae were active throughout most of the trapping period, reaching activity peaks in the summer and autumn of both years. Exceptional numbers of *Megasternum obscurum* and *Pterostichus madidus* adults were collected between July and September 1988. As mentioned earlier, the lack of grazing at this time was probably responsible for this, through the build up of plant material on pasture. The click beetle, *Agriotes obscurus*, showed a peak of adult activity in May and June of both years.

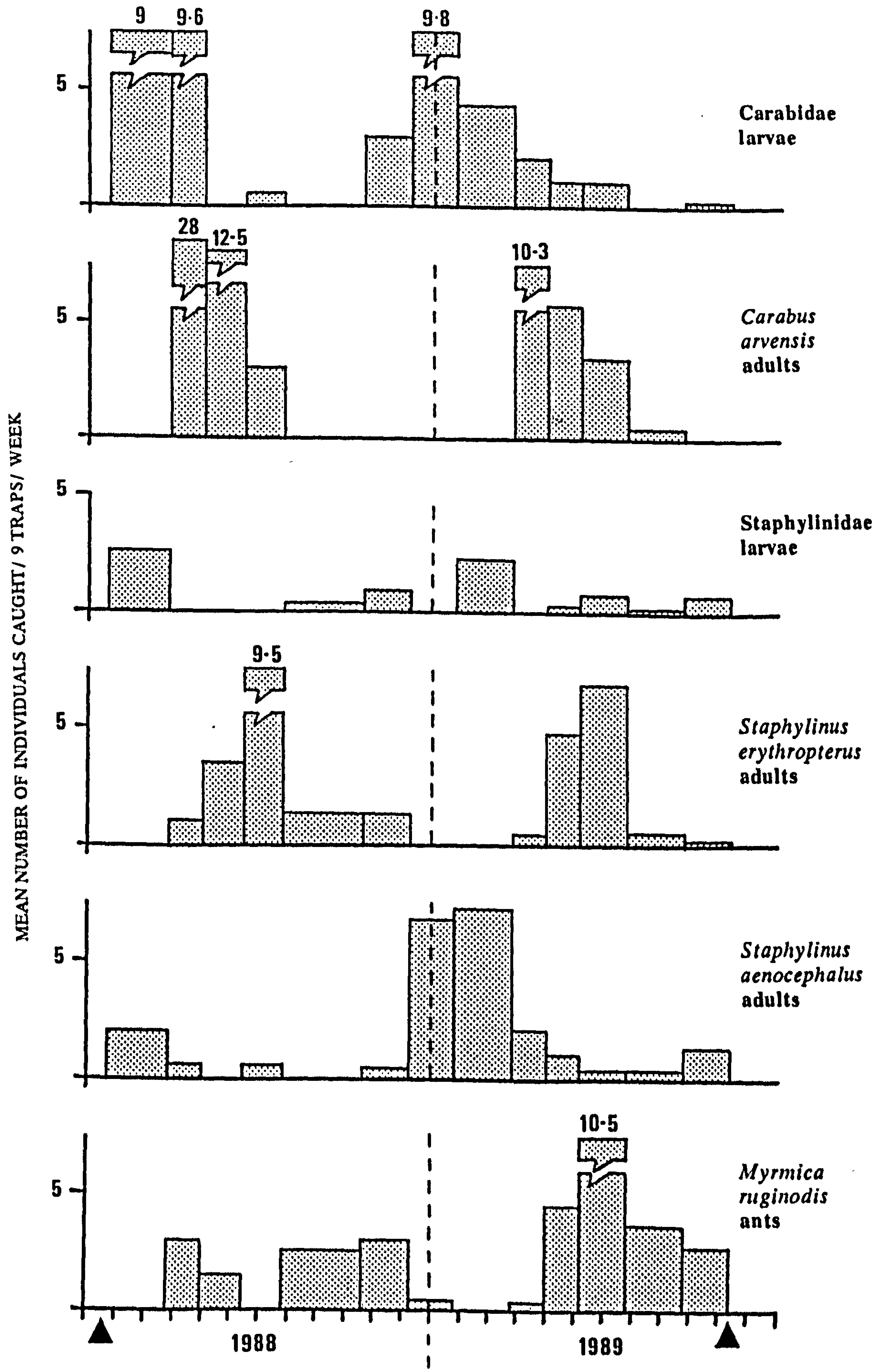


Fig. 4.4. Coille: mean number of each taxon caught per nine pitfall traps per week during each period between collection of the traps.
▲ denotes the beginning and end of pitfall trapping.

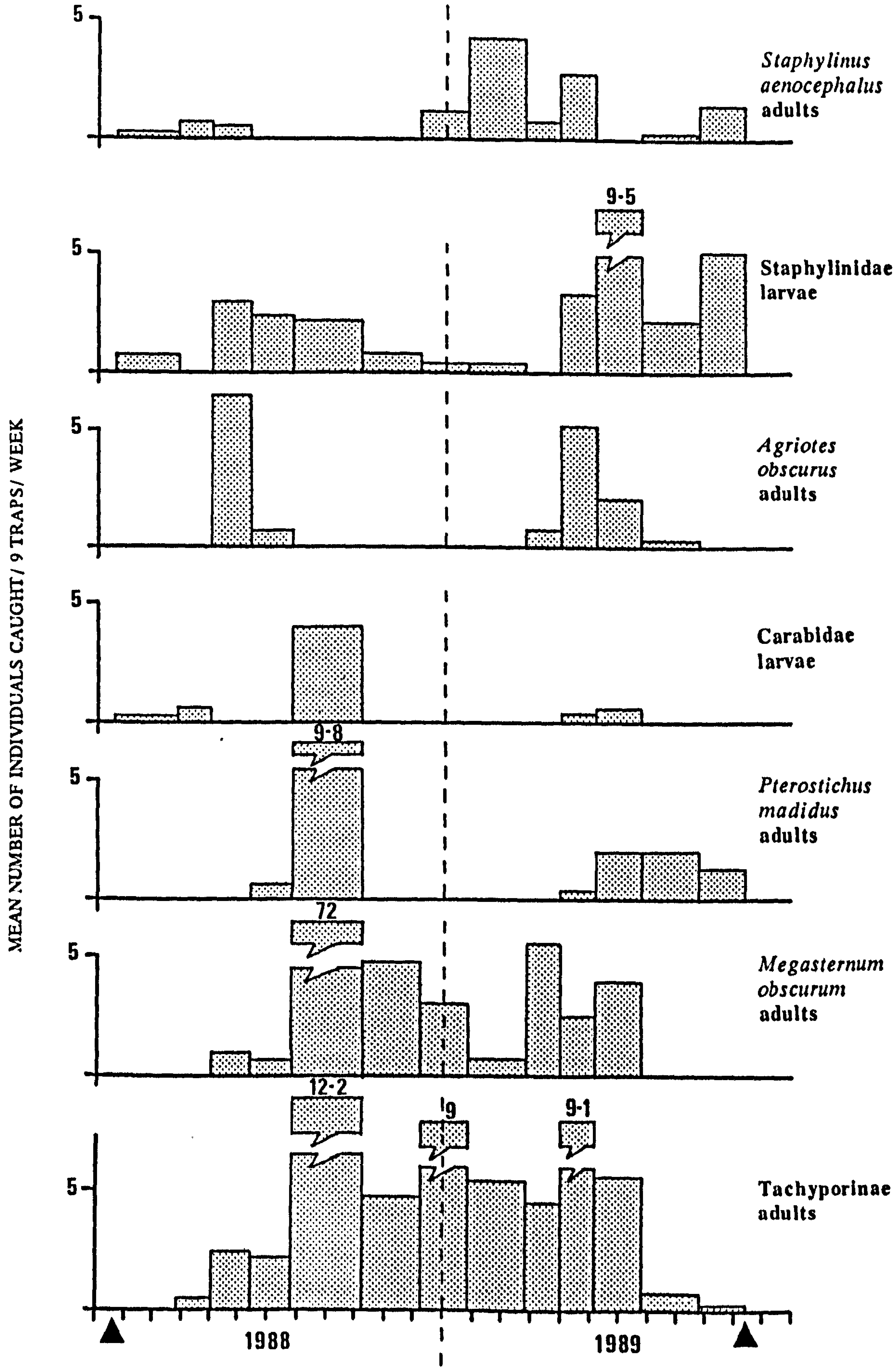


Fig. 4.5. Sanaigmore: mean number of each taxon caught per nine pitfall traps per week during each period between collection of the traps.
▲ denotes the beginning and end of pitfall trapping.

Ardnave (Fig. 4.6): large numbers of two species of ground beetle, *Calathus fuscipes* and *C. melanocephalus*, were collected in the summer and autumn of 1988, but these taxa were active only in small numbers in 1989. Conversely, Carabidae larvae only occurred in the traps at the beginning and end of 1988, but were found throughout the trapping period in 1989. Staphylinidae larvae were active during most of 1988 and 1989, peaking in October/November and May/June, respectively. Tachyporinae adults were collected in large numbers in the spring of both years. The dung beetle, *Aphodius foetidus*, was active during the winter of 1988/89, and the weevil, *Philopedon plagiatus*, showed an adult activity peak in May of both years.

Coul (Fig. 4.7): large numbers of *Calathus fuscipes* and *C. melanocephalus* adults were active during the summer and autumn of both years. Carabidae larvae were collected in numbers during winter and spring, and Staphylinidae larvae occured in the winter and spring of 1988/89. Adults of the large staphylinid, *Xantholinus glabratus*, were collected periodically throughout the trapping period. As at Ardnave, *Philopedon plagiatus* adults exhibited a peak of activity in May of both years. This was the only site at which earwigs, *Forficula auricularia*, were collected in any numbers, and they showed an activity peak in the summer and autumn of both years.

It would therefore appear that potential prey items were present throughout the year at all of the sites. However, the true availability of these taxa to the chough will be considered in the next section.

DISCUSSION

The most important advantage of pitfall traps is that they collect large samples of invertebrates throughout the time that they are in place (Coulson & Butterfield, 1985).

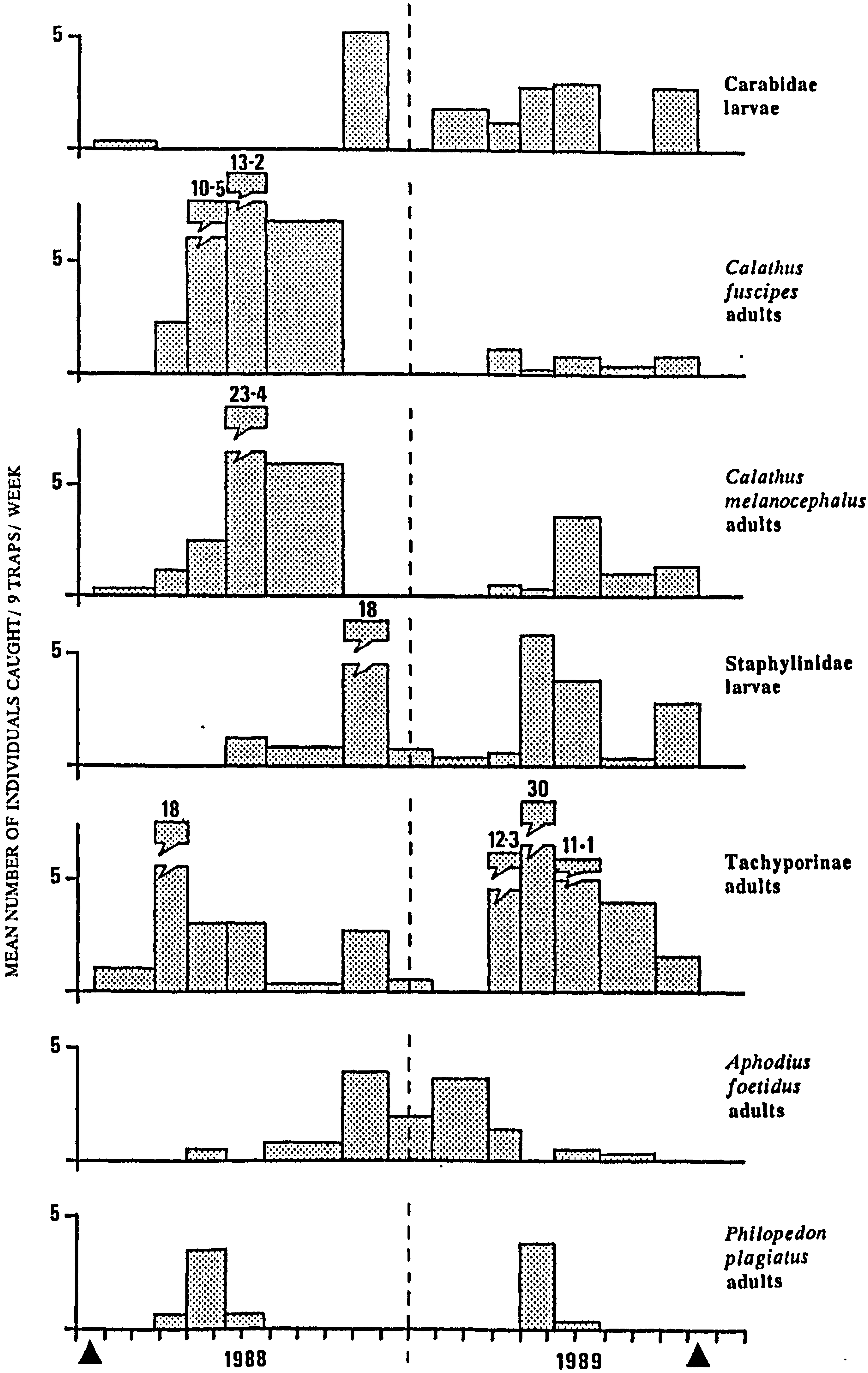


Fig. 4.6. Ardnave: mean number of each taxon caught per nine pitfall traps per week during each period between collection of the traps.
▲ denotes the beginning and end of pitfall trapping.

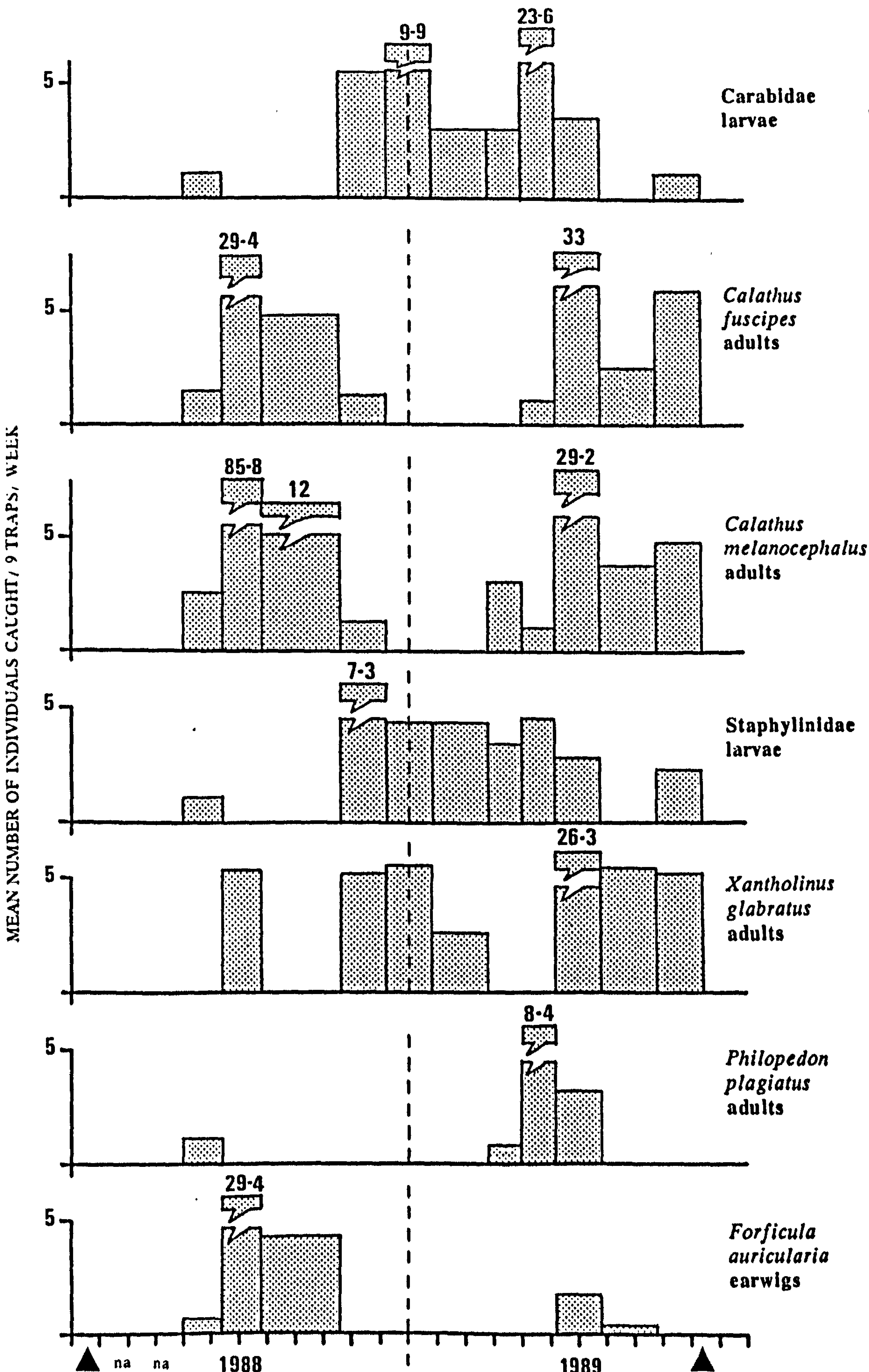


Fig. 4.7. Coul: mean number of each taxon caught per nine pitfall traps per week during each period between collection of the traps.
'na' - no data available for both these periods.
▲ denotes the beginning and end of pitfall trapping.

Pitfall trapping has been criticised as a sampling method, since the numbers of individuals caught depends on the activity of the species as well as their abundances (Southwood, 1978), but it has been shown that classifying sites by their pitfall catches is reasonable so long as the analysis is based on catch and not on absolute densities (Luff & Eyre, 1988). All factors relating to a site are reflected by pitfall catches, and the relative abundancies of species are important indicators of habitat type (Eyre *et al.*, 1989).

A further criticism of pitfall trapping is that captures are influenced by the nature of the vegetation (Greenslade, 1964; Luff, 1975). In this study, the grassland sites had a similar vegetation height for most of the trapping period, and therefore this source of error was minimised. The height of the heather layer on the peat site was higher, but the differences in fauna here, as compared to the grassland sites, were so great that they cannot be attributed to differences in the efficiency of the pitfall traps.

Although seasonal taxa assemblages were recognized, ordination of both presence/absence and abundance data indicate that the distribution of the invertebrate communities at these sites was primarily related to some feature of the soil. This was probably water content, since the sand grassland sites contained *Calathus fuscipes*, a well drained substrat~~e~~ species, whilst the peat and clay /um sites contained species indicative of damp and wet conditions e.g. *Olophrum* spp., *Pterostichus nigrita*, *P. versicolor*. Studies in uplands (Coulson & Butterfield, 1985; Luff *et al.*, 1989) and intensively managed grasslands (Eyre *et al.*, 1990b) have suggested that Carabidae community structure is usually related to soil structure and moisture.

Management practices have also been shown to have a profound effect on grassland beetle populations e.g. Eyre *et al.*, 1989; Luff & Eyre, 1988; Luff & Rushton, 1989; Rushton *et al.*, 1989. As mentioned previously, grazing intensity would appear to account for the separation of the end-groups in axis 2 of the ordination plot obtained from analysis of the abundance data.

Seasonality, therefore, does not appear to have as much effect on the surface-active invertebrate community at these sites as might initially have been expected. It is interesting to note that the sand grassland sites, which are used by chough throughout the year, do not appear to have a marked seasonal difference in taxa assemblages.

Finally, although surface-active potential food items for the chough appear to be present, at all the sites investigated, throughout the year, it must be borne in mind that these taxa may not necessarily be available to the birds. Many of the taxa may be nocturnal, while others may be adequately protected by the vegetation e.g. on the heather moorland.

CHAPTER FIVE:
ANALYSIS OF ISLAY SOIL FAUNA DATA

INTRODUCTION

Soil was sampled in order to establish the seasonal availability and abundance of potential prey items at each of the study sites. It should be noted that the soil samples were hand-sorted, even though small specimens are often lost (Southwood, 1978), because this method was considered sufficient to extract the larger specimens of interest as potential prey. In addition, hand-sorting of the samples on the island, although relatively time-consuming, meant that large numbers of soil cores did not have to be transported to the College.

METHODS

Data collection

The soil sampling regime is described for each site in Chapter 3. The dates on which a set of 20 soil cores (hereafter referred to as a subsample) was collected from each of the sites are shown in Table 5.1

Taxa were identified using the standard keys referred to in Chapter 4, and others such as Brauns (1954a & b); Brindle (1960; 1962a & b); Brindle & Smith (1978); van Emden (1945); Hennig (1948-52); Krivoseina (1962); Palm (1972); Skidmore (1985); and Theowald (1967).

The majority of taxa were inserted into the analyses at family level, even though some could be identified further. This was done because these genera and species occurred in such low numbers in the subsamples, that it was felt they would unduly distort the analyses if inserted at these levels. On this basis, a total of 34 taxa were identified

TABLE 5.1. Sites on Islay, with associated subsamples, from which soil sample data was obtained. See text for further information.

SITE	SUBSAMPLES (+ DATES OF COLLECTION)				
ARDNAVE	AA01 (180188)	AA02 (230388)	AA03 (270488)	AA04 (090688)	AA05 (150788)
(DRY)	AA06 (111088)	AA07 (301188)	AA08 (170189)	AA09 (070389)	
	AC01 (260489)	AC02 (070689)	AC03 (180789)	AC04 (120989)	AC05 (091189)
ARDNAVE	AB01 (230388)	AB02 (270488)	AB03 (090688)	AB04 (150788)	AB05 (111088)
(WET)	AB06 (301188)	AB07 (170189)	AB08 (070389)		
COILLE	BB01 (150188)	BB02 (220388)	BB03 (280488)	BB04 (110688)	BB05 (140788)
	BB06 (121088)	BB07 (011288)	BB08 (180189)	BB09 (100389)	
COUL	CW01 (160188)	CW02 (250388)	CW03 (290488)	CW04 (080688)	CW05 (130788)
	CW06 (101088)	CW07 (291188)	CW08 (180189)	CW09 (090389)	
	CW10 (250489)	CW11 (020689)	CW12 (170789)	CW13 (110989)	CW14 (081189)
SANAIGMORE	SA01 (180188)	SA02 (210388)	SA03 (280488)	SA04 (100688)	SA05 (130788)
	SA06 (121088)	SA07 (291188)	SA08 (180189)	SA09 (090389)	SA10 (270489)
	SA11 (140689)	SA12 (190789)	SA13 (120989)	SA14 (071189)	
	SB01 (190789)	SB02 (120989)	SB03 (071189)		
SMAUL	SM01 (280489)	SM02 (090689)			

(Table 5.2).

For similar reasons, subsamples containing less than 3 taxa were not included in the data set used in the analyses. This excluded 11 subsamples - 3 from the wet site (AB05, AB06 & AB08) and 1 from the dry area (AC04) at Ardnave; 4 (BB04, BB06, BB07 & BB08) from Coille; and 1 (SA06) from the main area, and 2 (SB02 & SB03), from the other half of the field, at Sanaigmore.

The final data set therefore contained abundance information on 34 taxa from 53 subsamples. Appendix 2 contains the taxa abundances for all 64 subsamples.

Classification and ordination

The 53 subsamples were classified by TWINSPAN (see Chapter 2), with the 'pseudo-species' function set to convert the frequency data into 4 classes: 1-4, 5-9, 10-24 and >24 individuals.

Taxa and subsamples were ordinated in two axes using DECORANA (see Chapter 2). All taxa were considered (a) equally, and (b) after downweighting of rare taxa.

After analyses of the data set, groups of subsamples were interpreted as representing distinct taxa assemblages. As in Chapter 4, the ordination scores derived from DECORANA were used to calculate the mean score, for the first two axes, of each end-group, and the typicalness measurements for each subsample within these end-groups.

Phenology

For each site, taxa considered potential chough prey items were extracted from the data set, and their abundances plotted for each date on which a subsample was taken.

TABLE 5.2. Taxa identified from soil samples on Islay. An abbreviation (7-8 letters) and a code number are shown for each taxon.

COLEOPTERA		
BYRRHIDAE		
Byrridae adult	BYRRADUL	6
CANTHARIDAE		
Cantharidae larvae	CANTLARV	7
CARABIDAE		
Carabidae adults	CARAADUL	8
" larvae	CARALARV	9
CHRYSOMELIDAE		
Chrysomelidae adult	CHRYADUL	12
CURCULIONIDAE		
Curculionidae adult	CURCADUL	13
" larvae	CURCLARV	14
DRYOPIDAE		
Dryopidae larvae	DRYOLARV	17
ELATERIDAE		
Elateridae adults	ELATADUL	19
" larvae	ELATLARV	20
HYDROPHILIDAE		
Hyrophilidae adults	HYDRADUL	21
Cercyon spp. larvae	CERCLARV	11
LEIODIDAE		
Leiodidae adults	LEIOADUL	22
SCARABAEIDAE		
Aphodius spp. adults	APHOADUL	1
" larvae	APHOLARV	3
Serica brunnea (L.) larvae	SERILARV	29
STAPHYLINIDAE		
Staphylinidae adults	STAPADUL	30
" larvae	STAPLARV	31
DIPTERA		
BIBIONIDAE		
Bibionidae larvae	BIBILARV	4
" pupa	BIBIPUPA	5
CECIDOMYIIDAE		
Cecidomyiidae larvae	CECILARV	10

Table 5.2 cont:

DOLICHOPODIDAE		
Dolichopodidae larvae	DOLILARV	16
MUSCIDAE		
Muscidae larvae	MUSCLARV	25
RHAGIONIDAE		
Rhagionidae larvae	RHAGLARV	26
SCATHOPHAGIDAE		
Scathophagidae pupa	SCATPUPA	27
SCIARIDAE		
Sciaridae larvae	SCIAADUL	28
TABANIDAE		
Tabanidae larvae	TABALARV	32
TIPULIDAE		
Tipulidae larvae	TIPULARV	33
TRICHOCERIDAE		
Trichoceridae larvae	TRICLARV	34
Diptera pupa	DIPTPUPA	15
OTHER		
Araneae - Spiders	SPIDERS	2
Diplopoda - Millipedes	MILIPEDE	24
Earthworms	EARTWORM	18
Lepidoptera larvae	LEPILARV	23

RESULTS

Classification and ordination

The classification of the abundance data is shown in Fig. 5.1. The majority of the Ardnave and Coul subsamples were separated from the majority of the Coille and Sanaigmore subsamples. No indicator taxa were identified for either of these groupings (see Chapter 2).

Using the above classification as a guide, it was clear from ordination of the data, without downweighting of rare taxa, that smaller groupings could be identified (Fig. 5.2).

Five end-groups were therefore recognized as representing distinct taxa assemblages. The subsamples within each end-group are shown in Table 5.3, and the frequency of occurrence of each taxon within these end-groups is given in Table 5.4. The mean number of taxa per subsample for each of the five end-groups are shown in Table 5.5.

The end-groups were described as follows:

End-group A: subsamples collected in January 1989 from the sand grassland sites at Ardnave and Coul, and in February 1989 from the dry site at Ardnave. These four subsamples were characterised by the presence of Bibionidae larvae, along with Tipulidae larvae, millipedes and earthworms.

End-group B: contained all the remaining subsamples from Coul and the the majority of those from the dry sites at Ardnave. At these times, earthworms and millipedes were prevalent in the soil at these sites, along with Staphylinidae and *Aphodius* spp. larvae.

End-group C: two subsamples collected in March 1988 and

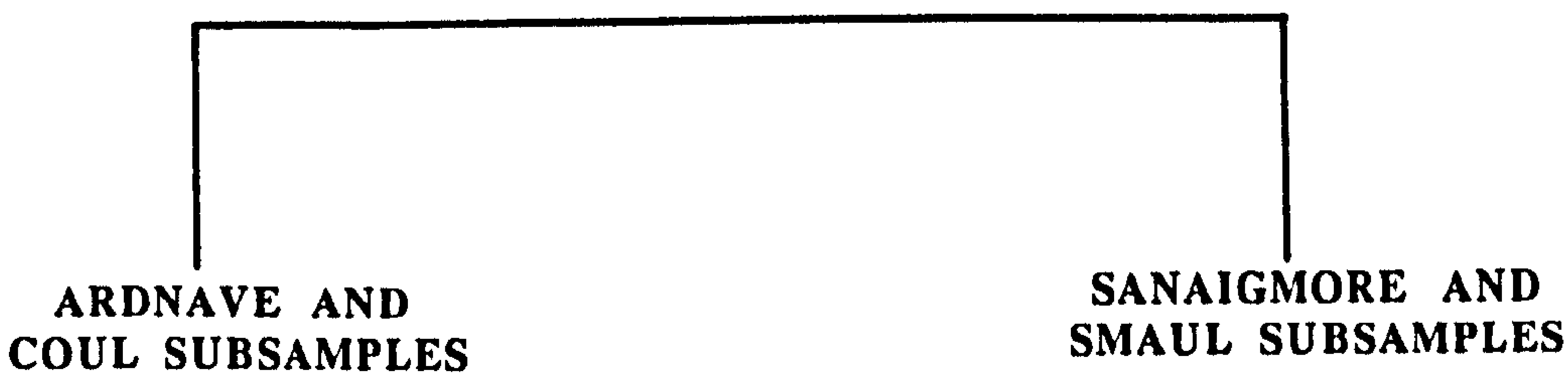


FIG. 5.1: Multivariate analysis of the soil data set: dendrogram showing the TWINSPAN classification of the abundance data.

TABLE 5.3. Multivariate analysis of the soil data set: end-groups, with associated subsamples, interpreted from TWINSPAN and DECORANA analysis of the soil sample abundance data. See Table 5.1 and text for further information.

END-GROUP	SUBSAMPLES								
A	AA08	AA09	AB07	CW14					
B	AA01	AA03	AA04	AA05	AA06	AA07	AC02	AC03	AC05
	CW01	CW02	CW03	CW04	CW05	CW06	CW07	CW08	CW09
	CW10	CW11	CW12	CW13					
C	AA02	AC01							
D	AB01	AB02	AB03	AB04	BB01	BB03	BB05	BB09	SA01
	SA04	SA05	SA10	SA11	SA12	SA14	SM01	SM02	
E	SA02	SA03	SA07	SA08	SA09	SA13	SB01	BB02	

TABLE 5.4. Multivariate analysis of the soil data set: the frequency of occurrence of taxa within the end-groups derived from TWINSPAN and DECORANA analyses of the abundance data, where a taxon occurs in >20% of the subsamples in one of the end-groups (D=21-40%; C=41-60%; B=61-80%; A=81-100%). The taxa order is derived from the TWINSPAN analysis and the abbreviations are as shown in Table 5.2.

TAXA	END-GROUP A	B	C	D	E
CARALARV	-	D	-	-	-
CURCADUL	-	-	C	-	-
MILIPEDE	B	A	-	-	-
SERILARV	-	-	C	-	-
APHOLARV	C	C	A	D	-
CURCLARV	D	D	-	-	-
BIBILARV	A	-	-	-	-
LEIOADUL	D	-	-	-	-
SCATPUPA	D	-	-	-	-
BIBIPUPA	-	-	A	-	-
EARTWORM	B	A	C	B	A
MUSCLARV	-	-	-	-	D
STAPLARV	-	C	-	D	-
TIPULARV	A	D	-	B	D
DOLILARV	C	D	C	C	D
CARAADUL	-	-	-	-	D
SPIDERS	-	-	-	C	-
ELATLARV	-	-	-	B	B
STAPADUL	-	D	-	D	D
LEPILARV	-	-	C	-	-
ELATADUL	-	-	-	-	D
SCIALARV	D	-	C	D	A
TABALARV	-	-	-	-	D
TRICLARV	-	-	C	-	-

TABLE 5.5. Multivariate analysis of the soil data set: number of subsamples, mean number of taxa per subsample (+ range) and mean typicalness measurements (+ range), in standard deviations of taxa turnover x 100 with and without downweighting of rare taxa, of the 5 end-groups interpreted from the TWINSPAN and DECORANA analyses of the abundance data.

END-GROUP	NUMBER OF SUBSAMPLES	MEAN NUMBER OF TAXA (+RANGE)	MEAN TYPICALNESS MEASUREMENTS (+RANGE) WITHOUT	& WITH DOWNWEIGHTING
A	4	6 (4-8)	26 (8-39)	28 (19-44)
B	22	6 (3-11)	44 (12-83)	47 (8-115)
C	2	6 (5-6)	26 (0)	26 (0)
D	17	6 (3-12)	33 (9-61)	41 (2-120)
E	8	6 (3-13)	26 (8-47)	32 (10-74)

April 1989, repectively, from the dry sites at Ardnave. Bibionidae pupae were characteristic of these subsamples, although both also contained *Aphodius* spp. larvae.

End-group D: contained the remaining subsamples from the wet area at Ardnave, along with the two subsamples from Smaul and the majority of those from Coille and Sanaigmore. Earthworms, and Tipulidae and Elateridae larvae were prevalent in these subsamples at these times.

End-group E: contained the remaining subsamples from Sanaigmore and Coille, with earthworms, and Sciaridae and Elateridae larvae prevalent.

Fig. 5.2 shows the axis 1 by axis 2 ordination plot, without downweighting of rare taxa, of the 53 subsamples used to classify end-groups. The mean scores, with associated standard errors, in each dimension are given for the five end-groups. The variance accounted for (based on eigenvalues of 0.734 and 0.584) was 56 and 44% for axes 1 and 2 respectively.

Axis 1 appears to be related to some feature of the soil, possibly moisture content, at each site, since the sand grassland sites (Ardnave and Coul) lie at one extreme, and the peat (Coille) and clay (Sanaigmore and Smaul) sites lie at the other. It is interesting to note that most of the subsamples from the wet area at Ardnave are associated with end-group D, at the 'wet' end of the axis.

Axis 2 appears to be related to seasonality, as end-groups D, E and A (containing a high proportion of 'winter/spring' subsamples) had the highest scores along this axis, whilst the subsamples with the lowest scores were those collected in the summer. As with the pitfall data, the majority of 'winter' and 'summer' subsamples from the sand grassland sites (end-group B) did not separate

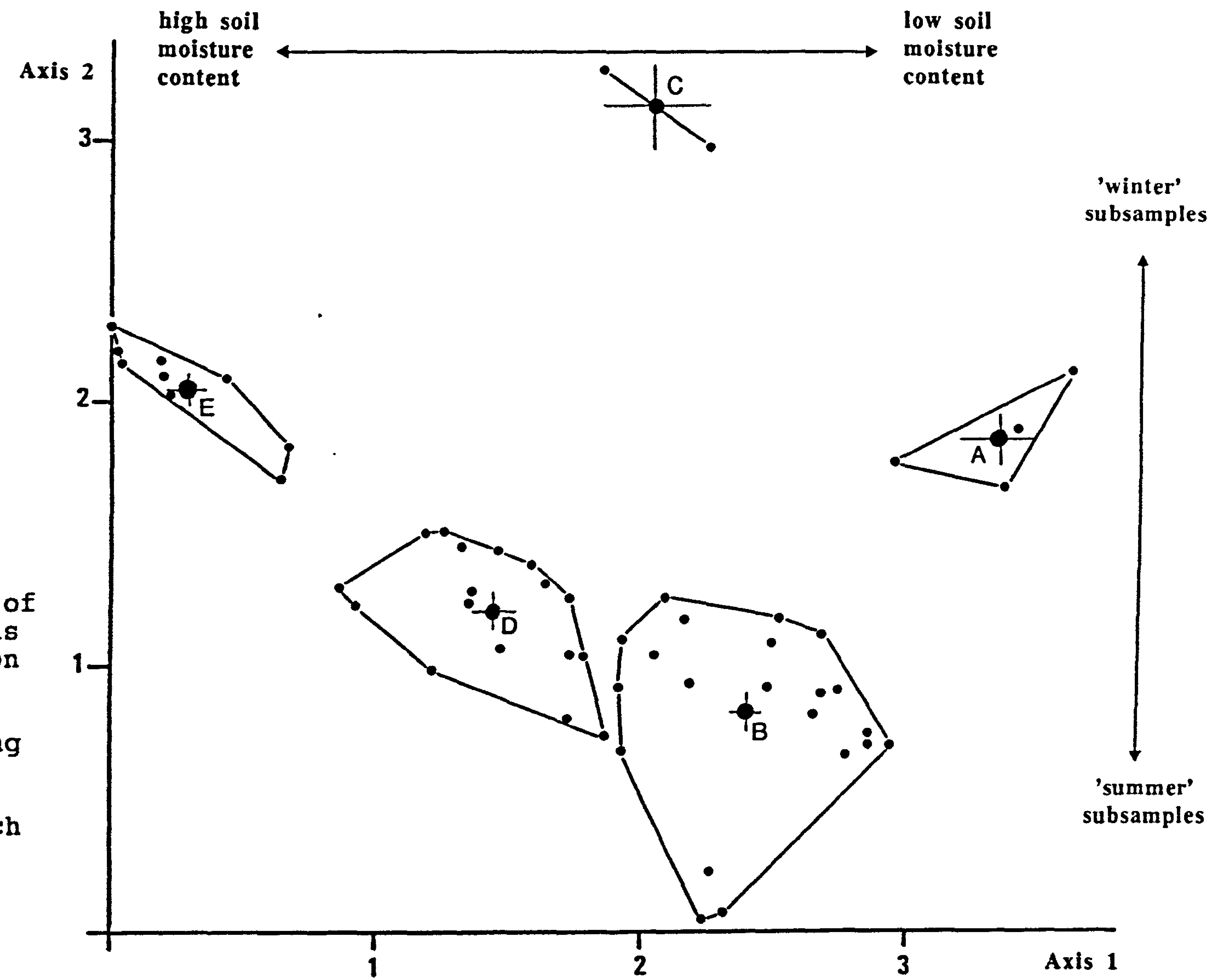


Fig. 5.2. Multivariate analysis of the soil data set: axis 1 by axis 2 plot of the DECORANA ordination of the abundance data, without downweighting of rare taxa. Polygons enclose space containing all the subsamples in each end-group (A-E). Mean score and associated standard error in each dimension of the ordination are given for the five end-groups.

well in axis 2, suggesting that possibly the taxa present in the soil at these sites did not differ markedly on a seasonal basis.

It was thought that the location of the end-groups in axis 2 could have been influenced more by the presence of rare taxa, than by the effect of seasonality. The data was therefore ordinated with downweighting of rare taxa, and the resulting plot is shown in Fig. 5.3. The variance accounted for was 66 and 34% for axes 1 and 2 respectively (based on eigenvalues of 0.698 and 0.363).

Compared to Fig. 5.2, it can be seen that after downweighting of rare taxa the end-groups were inverted in axis 1, and brought closer together in axis 2. However, both axes still appear to be related to moisture content and seasonality, respectively.

The mean typicalness measurements for each of the five end-groups are given in Table 5.5. All these values are small. This, together with the fact that the standard errors of the end-group mean scores on each axis are also small, relative to the distances between mean scores, would suggest that the end-groups as described from the analyses were valid.

Phenology

Figs. 5.4 - 5.8 give an indication of the seasonal occurrence in soil of some of the taxa considered potential chough prey items.

It should be remembered that the soil was only sampled to a depth of 10 cm. Therefore, the fact that a taxon was not present in a subsample should not be taken to imply that the taxon was absent from that particular site at that time. However, if such a taxon was present deeper in the soil it is possible that it would have been unavailable as potential prey for the chough (although choughs are quite

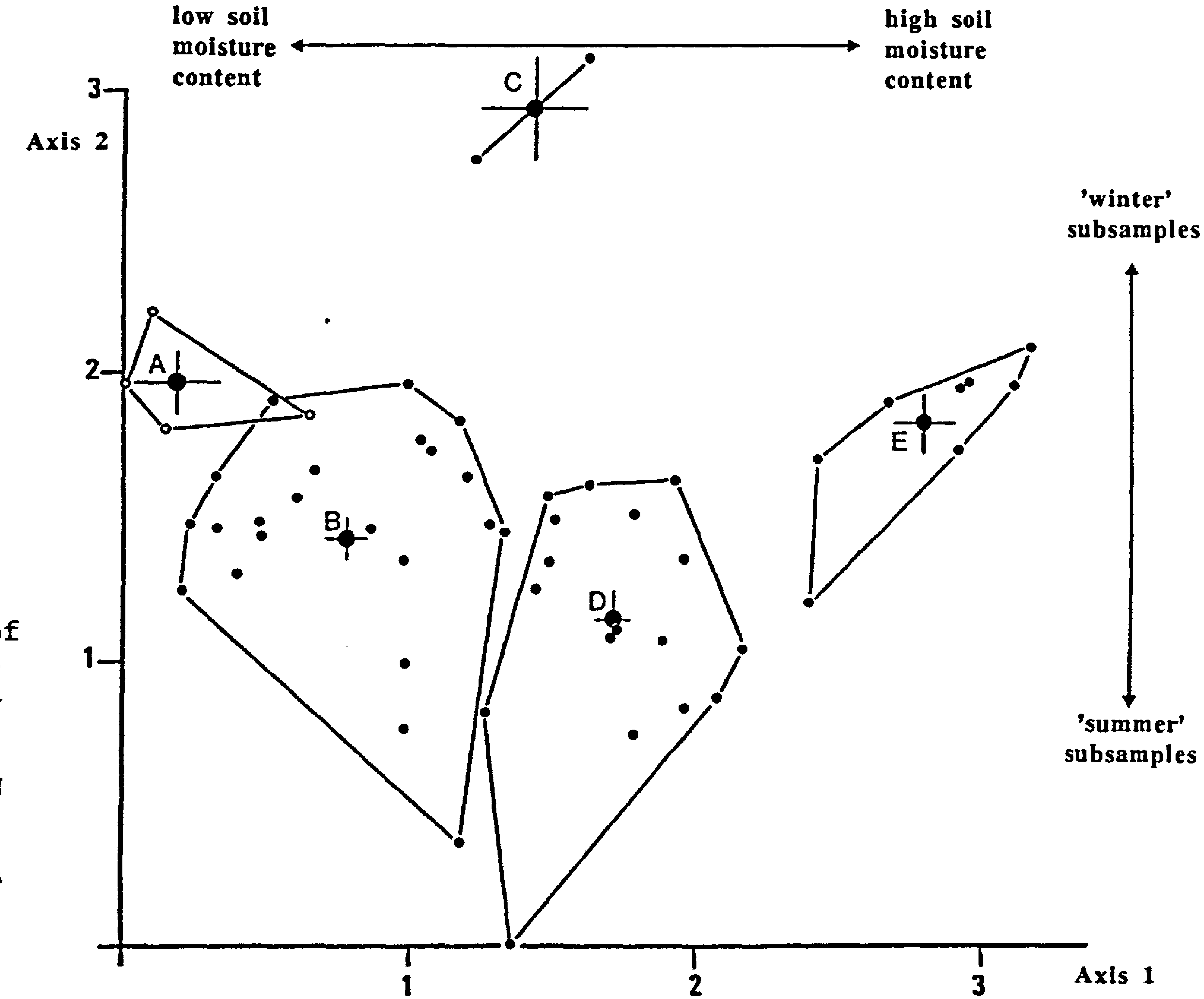


Fig. 5.3. Multivariate analysis of the soil data set: axis 1 by axis 2 plot of the DECORANA ordination of the abundance data, with downweighting of rare taxa. Polygons enclose space containing all the subsamples in each end-group (A-E). Mean score and associated standard error in each dimension of the ordination are given for the five end-groups.

capable of digging to depths greater than the length of their bills).

It should also be borne in mind that soil is a very difficult medium to sample accurately. The majority of the taxa were found in low numbers in the subsamples, therefore any minor fluctuations in the number of individuals of a taxon found at different times could have been due to sampling error. In addition, both Bibionidae and Sciaridae larvae are normally found aggregated in the soil, and therefore are more likely to be found in numbers.

Too much emphasis should therefore not be put on the numerical values for the majority of taxa in the following diagrams. The graphs should be regarded as showing posssible trends in taxa availability throughout the year, rather than absolute abundancies. Some of these taxa are discussed below.

Earthworms were found at all of the sites. The greatest numbers occurred on the wet site at Ardnave (Fig. 5.5), and this can probably be taken to imply that the population there was larger (or present more often in the top 10 cm of soil) than at the other sites. As would be expected, very few earthworms were found in the peat from Coille (Fig. 5.6). All the sites showed an apparent reduction in earthworm numbers during the summer months, and this could be a result of drier conditions forcing them deeper into the soil.

Tipulidae (mainly *Tipula paludosa* (Meigen)) larvae were also present at all of the sites, and their occurrence in the subsamples follows the expected trend i.e. they are present throughout most of the spring and summer, and 'disappear' in the autumn subsamples as a result of pupation and/or because the new population of larvae are still too small to be detected.

Bibionidae (mainly *Dilophus febrilis* (L.)) larvae and pupae were detected in the spring on the sand grassland sites at Ardnave (Figs. 5.4 & 5.5) and Coul (Fig. 5.7), and

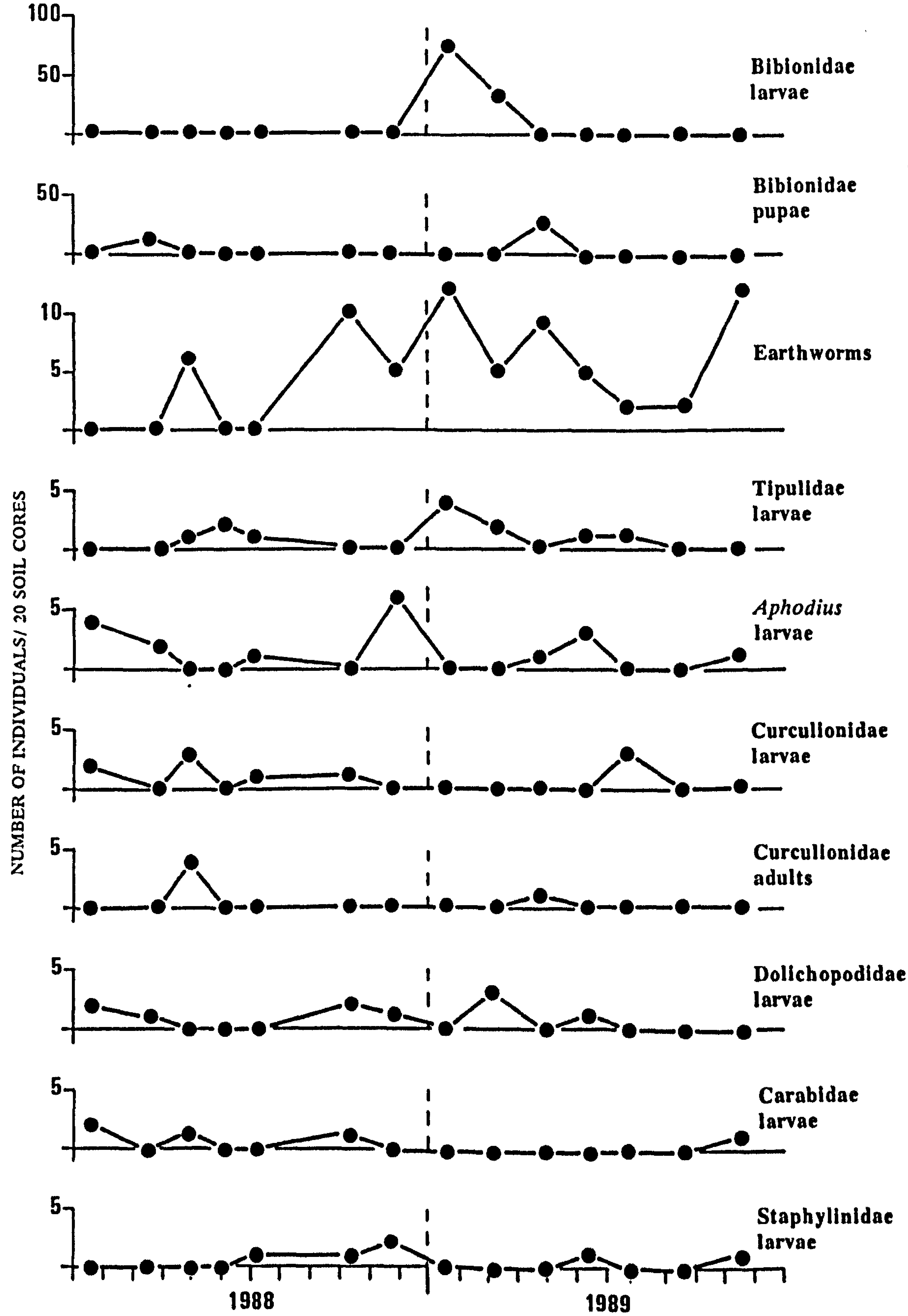


Fig. 5.4. Ardnave (dry): the total number of each taxon found in 20 soil cores on each sampling date.

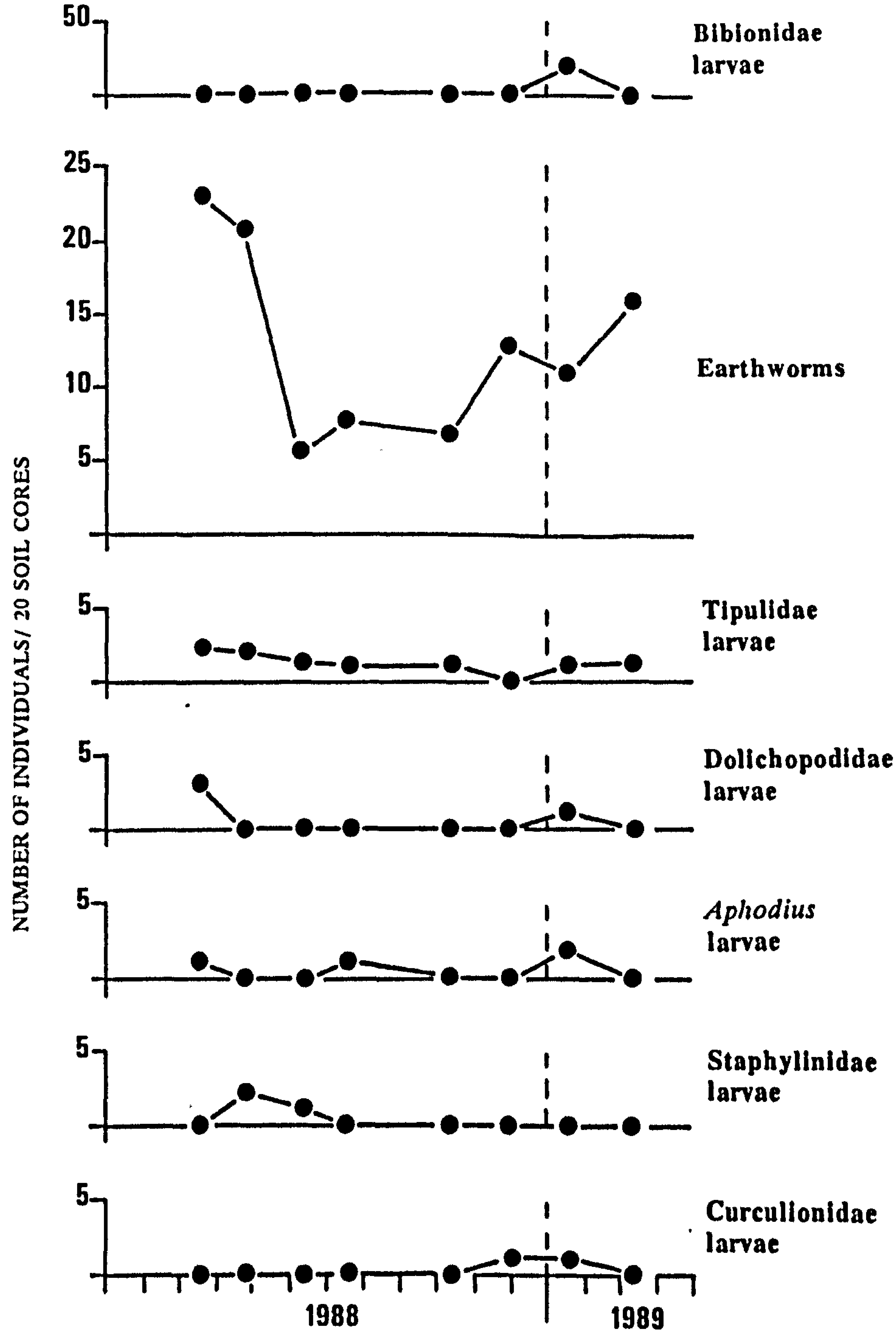


Fig. 5.5. Ardnave (wet): the total number of each taxon found in 20 soil cores on each sampling date.

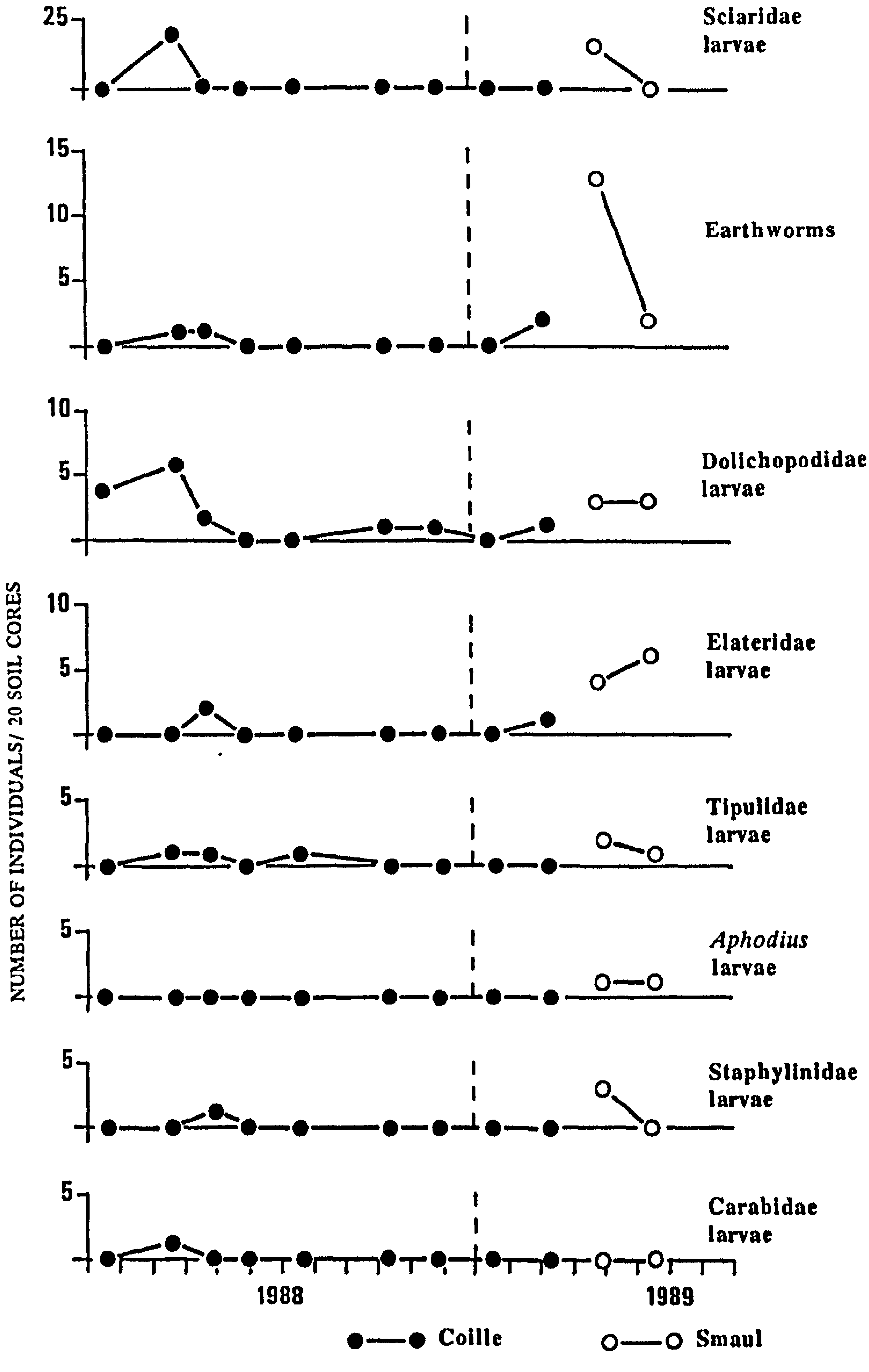


Fig. 5.6. Coille and Smaul: the total number of each taxon found in 20 soil cores on each sampling date.

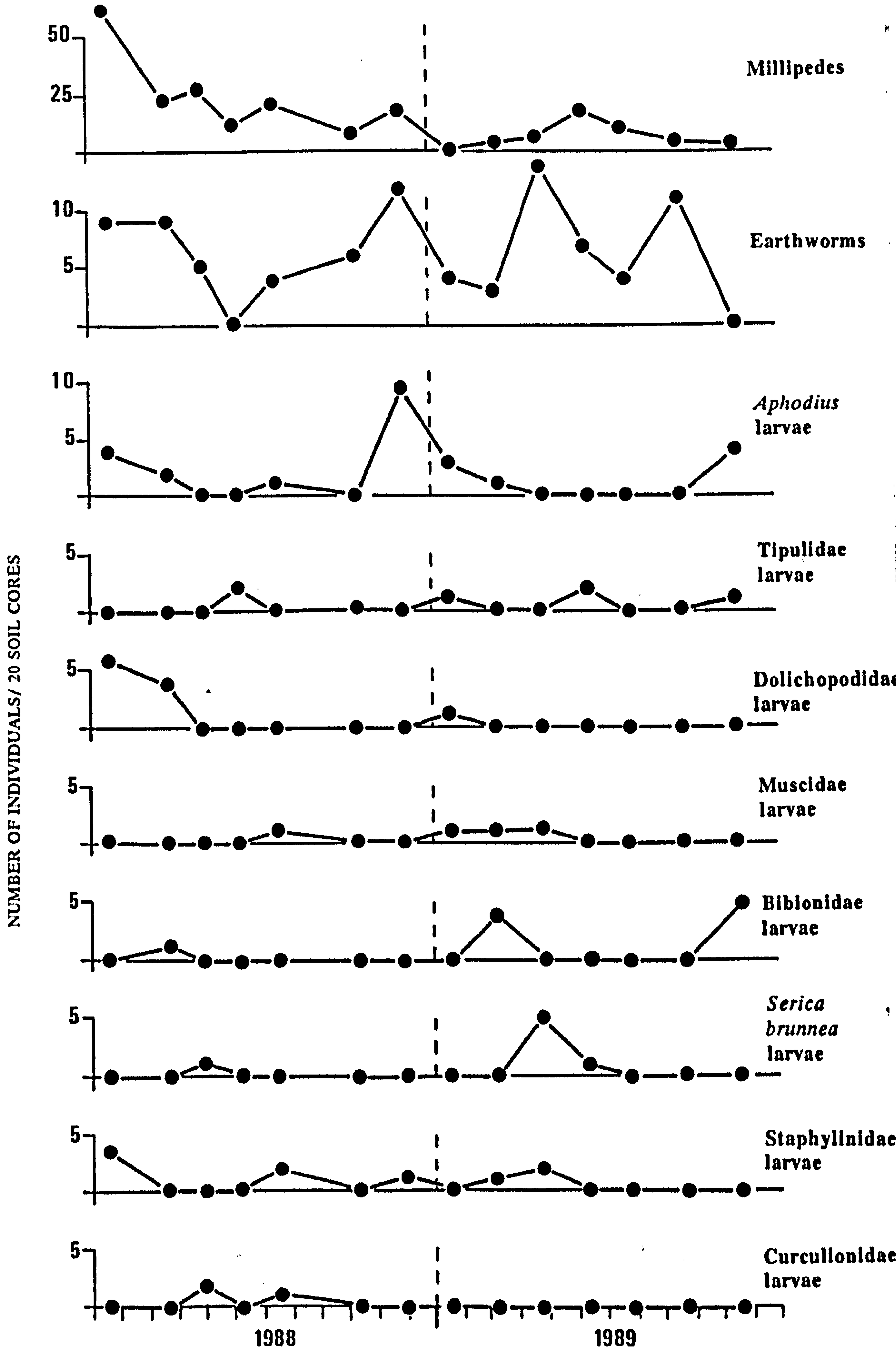


Fig. 5.7. Coul: the total number of each taxon found in 20 soil cores on each sampling date.

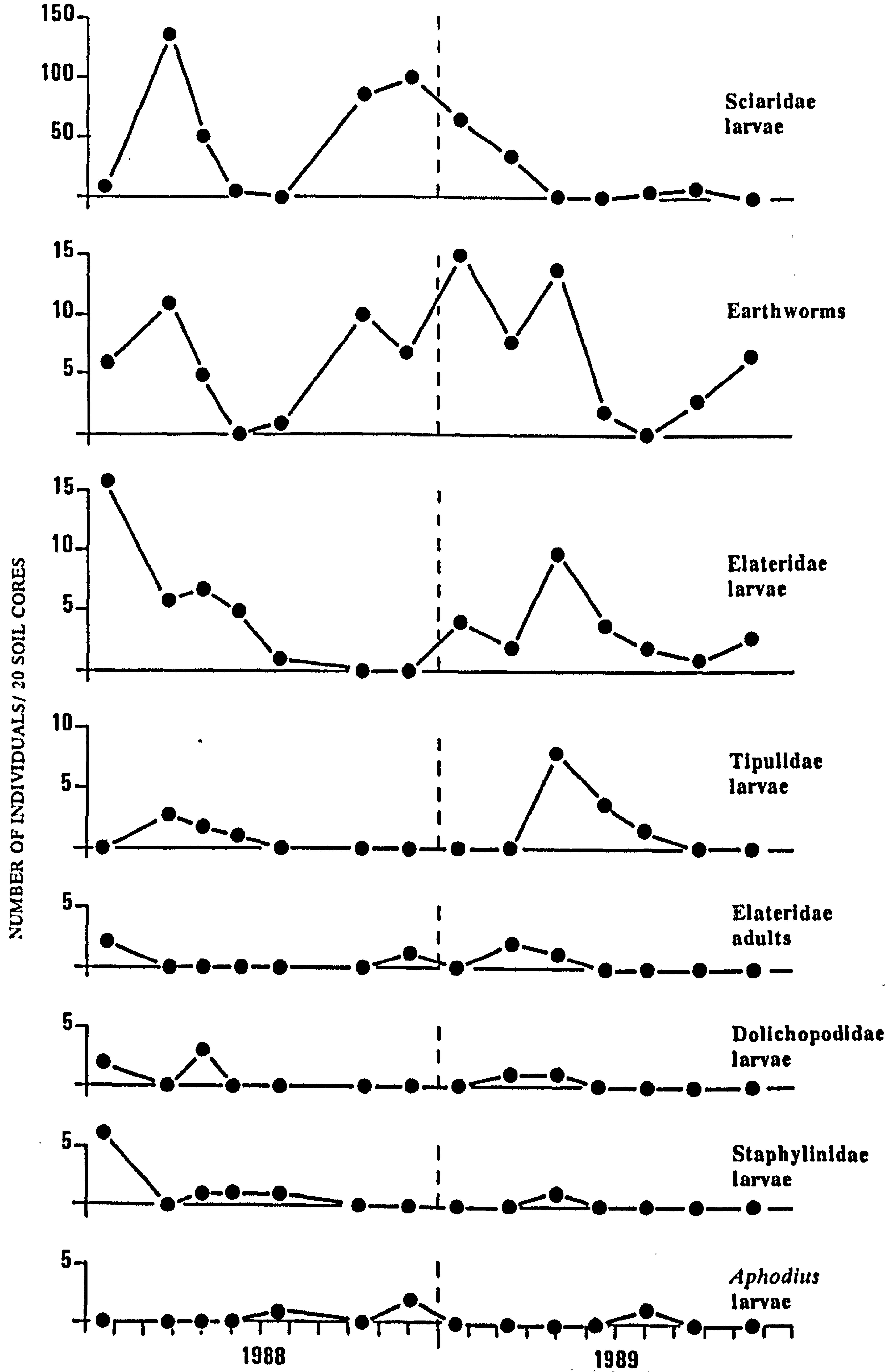


Fig. 5.8. Sanaigmore: the total number of each taxon found in 20 soil cores on each sampling date.

would therefore only appear to be large enough to be potentially available to the birds for a short period each year. The larvae large enough to be detected in November 1989 at Coul were *Bibio johannis* Haliday.

Aphodius spp. larvae were found in all of the pasture soils at some time during the two years. Their occurrence will be related to the grazing of these areas by sheep and cattle, allowing a sufficient time-lag, of course, for the disintegration of the dung and the movement of the larvae into the soil.

Dolichopodidae larvae were found at all of the sites, and their occurrence in the subsamples seems to be confined to the winter, and therefore wetter, months of each year.

The occurrence of Sciaridae larvae appears to follow the same pattern.

The majority of Elateridae larvae occurred in the old clay pastures at Sanaigmore (Fig. 5.8) and Smaul (Fig. 5.6). They seemed to show a similar trend to the earthworms i.e. a decrease in the summer months. While this must be related to adult emergence, it could also have been partly caused by the larvae moving deeper into the soil during the drier months.

DISCUSSION

As with the surface-active fauna, the primary factor influencing the soil fauna at these sites was probably water content, but organic matter, especially dung, content could also have been involved.

For example, Tipulidae larvae were prevalent at Ardnave, even though, during the summer at least, the soil here was very dry. However, as will be seen in the next chapter, tipulids at this site occurred regularly under cow dung, and it is therefore presumed that the high moisture content in the vicinity of such pats, even after the dung had dissappeared from 'surface view', accounts for this apparent contradiction. The sand grassland sites also contained *Aphodius* spp. and Scathophagidae larvae, which are associated with dung (Putman, 1983), and Bibionidae larvae, the ovipositing females of which may be attracted to soils high in organic content (Freeman & Lane, 1985).

Although the other sites contained Sciaridae larvae, which are common in situations containing decaying plant material (Freeman, 1983), few other taxa regarded as dung associating were found. Instead, taxa common in wet soils occurred, such as the predatory Tabanidae (Chvála *et al.*, 1972) and Dolichopodidae (d'Assis Fonesca, 1978) larvae, and root-feeding Elateridae (Palm, 1972) larvae.

From the results it would appear that the time of year is also an important factor governing soil fauna composition. At all the sites, the majority of taxa occurred in low numbers during the summer months. This accords well with the results obtained by Persson & Lohm (1977) from their study of a Swedish grassland soil. These authors found e.g. that the abundance of Dipteran (Nematocera and Brachycera) larvae, as well as total Coleoptera, fluctuated seasonally, with a minimum in June and a maximum in the 'winter' months (August - October). They concluded that the low densities in June coincided with adult emergence of many of species, and confirmed this by emergence trapping and sweep netting.

Such a relationship can also be discerned in this study. The reduction in numbers of Elateridae larvae in the soil at Sanaigmore during May and June of both years (Fig 5.8) is probably related to the increase in the numbers of adult *Agriotes obscurus* adults caught in pitfall traps at these times (Fig 4.5).

On the basis of abundances, soil would therefore not appear to be a good source of prey for the chough during the summer months. It must be borne in mind, however, that although the majority of taxa may only occur in low numbers during this period, as a result of seasonal increases in size, certain taxa, e.g. Tipulidae larvae, may be more 'worthwhile' prey items at this time time of year than at any other.

CHAPTER SIX:
ANALYSIS OF ISLAY COW DUNG DATA

INTRODUCTION

Previous studies (Chapter 2) stated that dung, especially from cattle, was an important source of food for the chough in Britain. It had also been implied that the practice of out-wintering cattle on Islay was important to the chough since it allowed the colonisation of cow dung by potential prey items throughout the winter months (Warnes, 1982). Cow dung was therefore sampled to establish the seasonal availability and abundance of potential prey items at each of the study sites.

METHODS

Data collection

Cow pats were sampled, when available, at each site during visits to the island. In addition, fresh pats were marked with canes to allow an estimate of their ages to be made when sampled on subsequent visits. Pats <3 or 4 weeks old were regarded as 'fresh'. The sampling method is described in Chapter 3, and the cow pats used in the study are shown in Table 6.1.

Taxa were identified using the standard keys referred to in previous chapters. A total of 54 taxa (Table 6.2) were identified for use in the analyses.

Appendix 3 contains the number of each taxon present in each pat. To avoid distortion of the analyses, pats containing less than 3 taxa were not included in the data set. Of the 229 pats sampled, 63 were therefore excluded, 89% of which were deposited on pasture between September and April i.e. during the 'winter' months.

TABLE 6.1. Cow pats sampled on Islay. A code number is given for each pat, together with sampling date and an estimate of age (F:<1 month old; A:1-2 months old; B:>2 months old). See text for further information.

SITE	PAT CODE NUMBERS - SAMPLING DATES & AGES				
ARDNAVE	A001-180188F	A002-180188F	A003-180188A	A004-180188A	A005-180188A
	A006-180188A	A007-230388F	A008-230388F	A009-230388B	A010-230388B
	A011-230388A	A012-230388A	A013-270488F	A014-270488F	A015-270488A
	A016-270488A	A017-270488B	A018-270488B	A019-270488A	A020-270488A
	A021-090688F	A022-090688F	A023-090688B	A024-090688B	A025-090688A
	A026-090688A	A027-150788F	A028-150788F	A029-150788B	A030-150788B
	A031-150788B	A032-150788A	A033-150788A	A034-111088F	A035-111088F
	A036-111088B	A037-301188F	A038-301188F	A039-301188A	A040-301188A
	A041-170189F	A042-170189F	A043-170189A	A044-170189A	A045-170189A
	A046-170189B	A047-070389F	A048-070389F	A049-070389B	A050-070389B
	A051-260489F	A052-260489F	A053-260489F	A054-260489A	A055-260489A
	A056-030689F	A057-030689F	A058-030689F	A059-030689F	A060-180789F
	A061-180789F	A062-180789A	A063-180789A	A064-180789B	A065-180789B
	A066-120989F	A067-120989F	A068-120989F	A069-120989F	A070-120989A
	A071-120989A	A072-091189F	A073-091189F	A074-091189A	A075-091189A
	A076-091189A	A077-091189A	A078-091189A	A079-091189A	A080-091189B
	A081-091189B	A082-091189B	A083-091189B		
COILLE	B001-150188F	B002-150188F	B003-150188A	B004-150188A	B005-150188B
	B006-150188B	B007-220388F	B008-220388F	B009-220388B	B010-220388B
	B011-220388B	B012-220388B	B013-280488F	B014-280488F	B015-280488B
	B016-280488B	B017-280488A	B018-280488A	B019-110688F	B020-110688F
	B021-110688A	B022-110688A	B023-110688B	B024-110688B	B025-110666B
	B026-110688B	B027-140788F	B028-140788F	B029-140788A	B030-140788A
	B031-140788B	B032-140788B	B033-121088F	B034-121088F	B035-011288F
	B036-011288F	B037-011288A	B038-011288A	B039-180189F	B040-180189F
	B041-180189A	B042-100389A	B043-100389A	B044-040689F	B045-040689F
	B046-040689A	B047-040689A	B048-180789F	B049-180789F	B050-180789A
	B051-180789A	B052-071189F	B053-071189F	B054-071189F	B055-071189F
	B056-071189B	B057-071189B	B058-071189B	B059-071189B	
COUL	C001-160188F	C002-160188F	C003-160188A	C004-160188A	C005-160188A
	C006-160188A	C007-250388F	C008-250388F	C009-250388F	C010-250388F
	C011-250388A	C012-250388A	C013-290488F	C014-290488F	C015-290488A
	C016-290488A	C017-290488A	C018-290488B	C019-080688F	C020-080688F
	C021-080688B	C022-080688B	C023-080688A	C024-080688A	C025-130788F
	C026-130788F	C027-130788A	C028-130788A	C029-130788B	C030-130788B
	C031-130788B	C032-130788B	C033-180189F	C034-180189F	C035-180189A
	C036-180189A	C037-090389F	C038-090389F	C039-090389A	C040-090389A
	C041-250489F	C042-250489F	C043-250489F	C044-250489F	C045-250489A
	C046-250489A	C047-020689F	C048-020689F	C049-020689A	C050-020689A
	C051-170789A	C052-170789A	C053-170789B	C054-170789B	C055-110989F
	C056-110989F	C057-110989B	C058-110989B	C059-081189F	C060-081189F
	C061-081189A	C062-081189A	C063-081189A	C064-081189A	
SANAIGMORE	S001-180188F	S002-180188F	S003-180188A	S004-180188A	S005-210388F
	S006-210388F	S007-210388B	S008-210388B	S009-210388B	S010-210288B
	S011-280488A	S012-280488A	S013-280488B	S014-280488B	S015-100688B
	S016-100688B	S017-100688B	S018-291188F	S019-291188F	S020-180189F
	S021-180189F	S022-090389A	S023-090389A		

TABLE 6.2. Taxa identified in the cow pats sampled on Islay. An abbreviation (7-8 letters) and a code number are given for each taxon.

COLEOPTERA		
Cantharidae larvae	CANTLARV	15
Carabidae adults	CARAADUL	16
" larvae	CARALARV	17
Chrysomelidae larvae	CHRYLARV	21
Curculionidae larvae	CURCLARV	22
Philopedon plagiatus (Schaller) adults	PHILPLAG	38
Elateridae larvae	ELATLARV	25
Geotrupidae adults	GEOTADUL	29
" larvae	GEOTLARV	30
Hydrophilidae adults	HYDRADUL	31
" larvae	HYDRLARV	32
Leiodidae adults	LEIOADUL	33
Ptiliidae adults	PTILADUL	41
Scarabaeidae		
Aphodius ater (Degeer) adults	APHOATER	3
A. *contaminatus* (Herbst) adults	APHOCONT	4
A. *depressus* (Kugelann) adults	APHODEPR	5
A. *fimetarius* (L.) adults	APHOFIME	6
A. *foetidus* (Herbst) adults	APHOFOET	7
A. *fossor* (L.) adults	APHOFOSS	8
Aphodius spp. larvae	APHOLARV	9
A. *prodromus* (Brahm) adults	APHOPROD	10
A. *rufipes* (L.) adults	APHORUFI	11
A. *rufus* (Moll) adults	APHORUFU	12
A. *sphacelatus* (Panzer) adults	APHOSPAC	13
Staphylinidae adults	STAPADUL	50
" larvae	STAPLARV	51
DIPTERA		
Anisopodidae larvae	ANISLARV	1
Anthomyiidae larvae	ANTHLARV	2
Bibionidae larvae	BIBILARV	14
Cecidomyiidae larvae	CECILARV	18
Ceratopogonidae larvae	CERALARV	19

Table 6.2 cont:

Chironomidae larvae	CHIRLARV	20
Dolichopodidae larvae	DOLILARV	23
Empidae larvae	EMPILARV	26
Fanniidae larvae	FANNLARV	27
Muscidae larvae	MUSCLARV	36
" puparia	MUSCPUPA	37
Psychodidae larvae	PSYCLARV	39
" pupae	PSYCPUPA	40
Scathophagidae larvae	SCATLARV	42
" puparia	SCATPUPA	43
Scatopsidae larvae	SCATOPSI	44
Sciaridae larvae	SCIALARV	45
Sepsidae larvae	SEPSLARV	46
Sphaeroceridae larvae	SPHALARV	47
" puparia	SPHAPUPA	48
Stratiomyidae larvae	STRALARV	52
Tipulidae larvae	TIPULARV	53
Trichoceridae larvae	TRICLARV	54
OTHER		
Araneae - spiders	SPIDERS	48
Dermaptera - *Forficula auricularia* L.	FORFAURI	28
Diplopoda - millepedes	MILIPEDE	35
Lepidopteran larvae	LEPILARV	34
Oligochaeta - earthworms	EARTWORM	24

The final data set therefore contained abundance information on 54 taxa from 166 pats.

Classification and ordination

The 166 pats were classified using TWINSPAN (see Chapter 2), with the 'pseudo-species' function set to convert the abundance data into 4 classes: 1-4, 5-9, 10-24 and >24 individuals.

Taxa and pats were ordinated in three axes using DECORANA (see Chapter 2), without downweighting of rare taxa.

Phenology

Seasonal differences in the fauna associated with cow pats in this area of Islay were evident from the results. Using pats deposited at Ardnave as representative examples, the differences in fauna were shown by extracting the information for four different deposition dates from the data set.

RESULTS

Classification

The classification of the data set is given in Fig. 6.1, together with the indicator taxa at each division. Five end-groups were recognized as representing distinct taxa assemblages. The pats within each end-group are shown in Table 6.3, and the frequency of occurrence of each taxon within these end-groups is given in Table 6.4.

Age and deposition date appear to interact in determining the separation of the pats. The end-groups were described as follows:

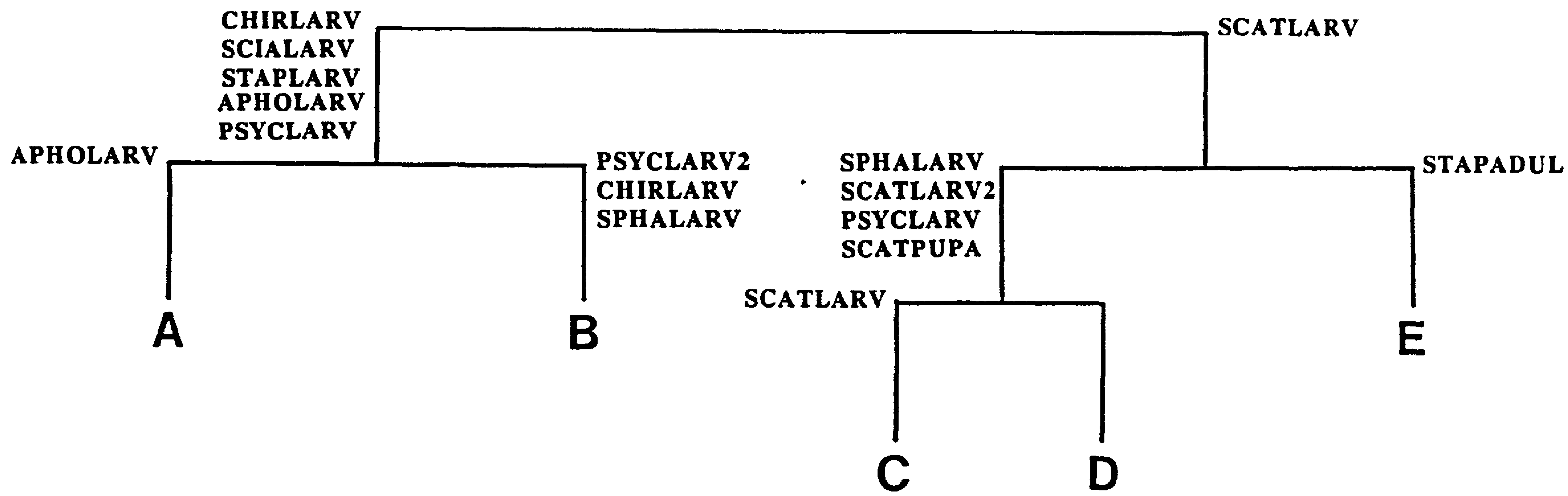


Fig. 6.1. Multivariate analysis of the dung data set: dendrogram showing the five end-groups interpreted from the TWINSPAN classification of the abundance data. The indicator taxa at each division are shown (abbreviations as in Table 6.2), and the numbers indicate the 'pseudo-species' class where it is other than 1.

TABLE 6.3. Multivariate analysis of the dung data set: end-groups, with associated cow pats, interpreted from TWINSPAN analysis of the abundance data. See Table 6.1 and text for further information.

END-GROUP	COW PATS							
A	A015	A016	A017	A018	A020	A024	A025	A026
	A030	A031	A032	A033	A046	A047	A048	A050
	A052	A057	A058	A059	A062	A063	A076	A081
	B007	B011	B015	B016	B023	B029	B042	B050
	B051							
	C017	C018	C021	C022	C023	C024	C027	C028
	C029	C030	C037	C049	C051	C052	C057	C058
	S001	S005	S012	S015	S016	S017		
B	A003	A004	A005	A006	A011	A012	A034	A036
	A039	A040	A043	A044	A054	A070	A071	A074
	A075	A077						
	B003	B004	B005	B006	B009	B010	B012	B017
	B018	B021	B022	B030	B031	B032	B036	B037
	B038	B044	B045	B057				
	C003	C004	C005	C006	C011	C035	C036	C061
	C063	C064						
	S003	S004	S007	S008	S009	S010	S011	S014
	S018	S019	S022					
C	A045	A067	A068	A069	A078			
	B047	B052	B055					
	C009	C041	C042	C043	C044	C059	C060	
D	A019	A056						
	B048	B049						
	C010	C040	C048					
E	A007	A008	A021	A029	A051	A053	A055	A060
	A061	A066						
	B008	B013	B014	B027	B028	B033	B034	B041
	C013	C014	C020	C026	C031	C045	C046	C047
	C050	C053	C054					
	S013							

TABLE 6.4. Multivariate analysis of the dung data set: the frequency of occurrence of taxa within the end-groups interpreted from TWINSPAN analysis of the abundance data, where a taxon occurs in >20% of the cow pats in one of the end-groups (D=21-40%; C=41-60%; B=61-80%; A=81-100%). The taxa order is derived from the TWINSPAN analysis and the abbreviations are as shown in Table 6.2.

TAXA	END-GROUPS				
	A	B	C	D	E
PSYCLARV	-	B	D	C	-
CHIRLARV	D	B	-	D	-
SCIALARV	D	D	-	-	-
APHOLARV	B	-	D	-	-
TIPULARV	D	-	-	-	-
DOLILARV	D	D	-	-	-
STAPLARV	C	C	-	B	-
MILIPEDE	D	-	-	D	D
EARTWORM	C	C	D	-	D
HYDRLARV	-	D	-	C	-
SCATPUPA	-	-	D	D	-
SPHALARV	-	D	B	A	-
ANTHLARV	-	-	D	C	-
SCATLARV	-	-	A	-	-
SEPSLARV	-	-	-	C	-
APHORUFI	-	-	-	D	-
APHOSPAC	-	-	-	-	D
APHOFIME	-	-	-	C	D
HYDRADUL	-	-	D	-	C
STAPADUL	D	D	-	C	B

TABLE 6.5. Multivariate analysis of the dung data set: position, with associated SE, on each DECORANA axis and distances between centroids of each end-group interpreted from TWINSPAN analysis of the abundance data. All positions are in DECORANA axis units.

END-GROUP	POSITION			DISTANCE FROM END-GROUP			
	Axis: 1	2	3	B	C	D	E
A	245±9	336±8	210±8	47	152	168	164
B	280±12	366±6	201±4		194	212	208
C	96±18	312±22	228±5			144	110
D	170±13	191±17	250±7				111
E	130±14	226±17	169±21				

End-group A: a group of old pats, the majority of which were deposited in the 'summer' months (March/April - September/October). *Aphodius* spp. larvae were prevalent in and below these pats, along with earthworms, and Staphylinidae and Tipulidae larvae.

End-group B: a group of old pats, the majority of which were deposited in the 'winter' months (September/October - March/April). Psychodidae and Chironomidae larvae were active in and below these pats, along with Staphylinidae larvae and earthworms.

End-group C: a group of fresh pats, mainly deposited either in 'spring' (March/April) or 'autumn' (September/October). Scathophagidae and Sphaeroceridae larvae were prevalent in and below these pats.

End-group D: a small group of fresh pats, the majority of which were deposited in 'midsummer' (June/July). These pats contained the most diverse fauna e.g. Staphylinidae adults and larvae, *Aphodius fimetarius* adults, and Anthomyiidae, Hydrophilidae, Psychodidae, Sepsidae and Sphaeroceridae larvae.

End-group E: a collection of 'summer' pats that were very fresh when sampled. Staphylinidae and Hydrophilidae adults were among the few taxa active in and below these pats.

Ordination

Fig. 6.2 shows the centroids of the end-groups interpreted from the TWINSPAN analysis plotted against the first three DECORANA axes. Their positions (with associated standard errors) and relative distances from one another are given in Table 6.5. The variance accounted for (based on eigenvalues of 0.832, 0.607 and 0.552) was 42, 30 and 28% for axes 1, 2 and 3, respectively.

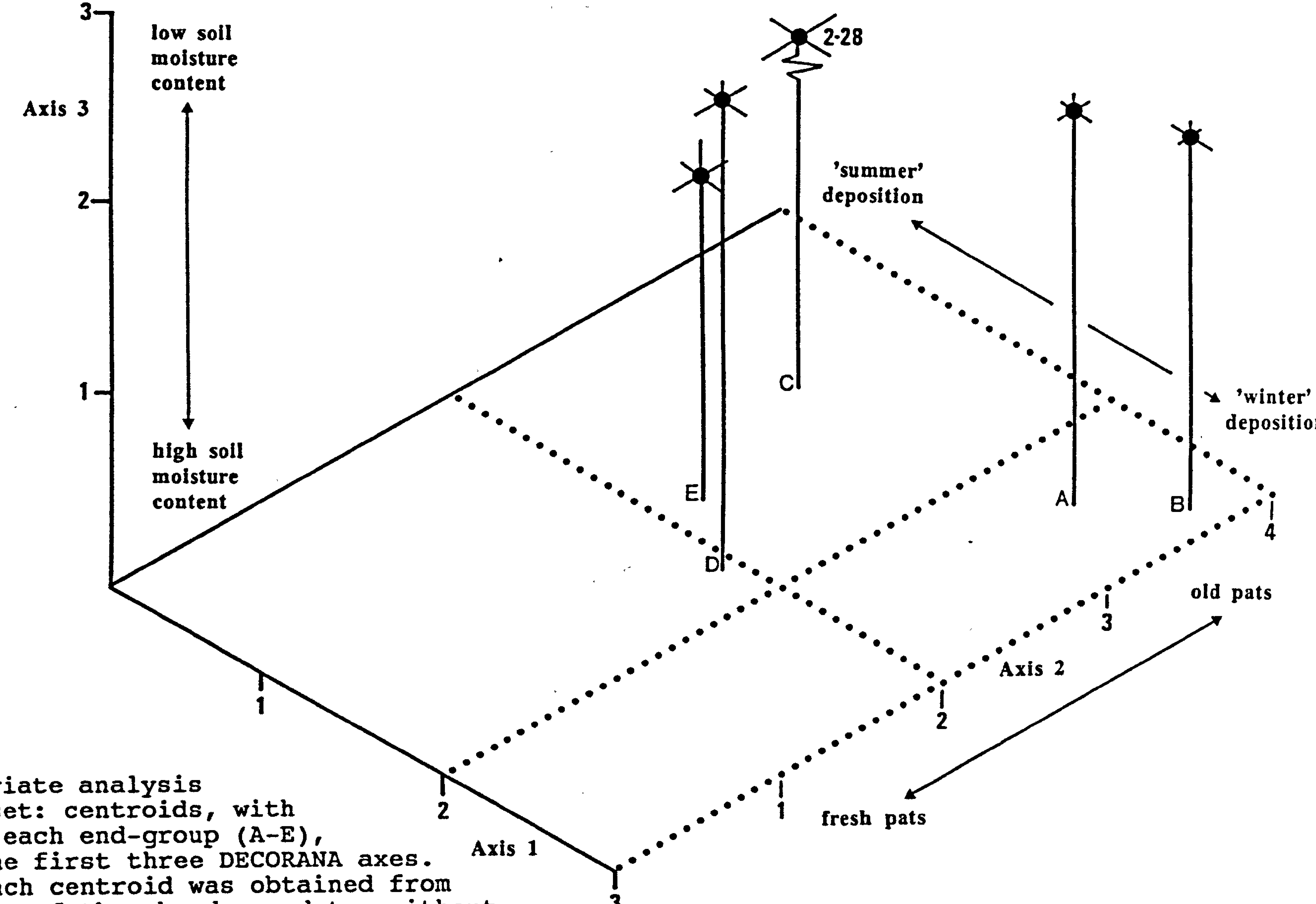


Fig. 6.2. Multivariate analysis of the dung data set: centroids, with associated SE, of each end-group (A-E), plotted against the first three DECORANA axes. The position of each centroid was obtained from DECORANA ordination of the abundance data, without downweighting of rare taxa.

The ordination of the pats in each axis appears to be determined by a combination of deposition date, age and sample site.

Axis 1 appears to be largely related to deposition date, as the pats deposited during the 'summer' months occur towards the lower end of the axis, while those deposited in the 'winter' months occur towards the other.

Axis 2 appears to be related to the age of the pats, since the fresh pats lie at the lower end of the axis, and the older pats lie towards the other.

Axis 3 appears to be related to some feature of the soil, possibly moisture content, at each site, as the pats on sand grassland (Coul and Ardnave) lie at one extreme of this axis, while those on clay (Sanaigmore) and peat (Coille) lie at the other.

From the calculated distances between end-groups (Table 6.5) it can be seen that end-groups A and B were very close. However, the standard errors of the mean pat scores on each axis were small, relative to the distance betwen centroids, indicating that the definitions of these end-groups were valid.

Phenology

Seasonal variations in the fauna associated with the cow pats were evident from the data. As the seasonal differences were broadly similar at each site, pats deposited at Ardnave were considered to be representative examples. The fauna associated with these pats is given below for four different deposition dates.

(a) Pats deposited in November:

No beetles were found in fresh pats, suggesting that there was very little beetle activity at this time of year. Flies were active, as the pats were found to contain large numbers of Bibionidae, Psychodidae, Sphaeroceridae, Chironomidae and Trichoceridae larvae in January, 1-2 months after deposition.

(b) Pats deposited in March:

Beetles appear to become active around this time of year, and fresh pats were highly attractive to Hydrophilidae and *Aphodius* spp. (at Ardnave A. *fimetarius* and A. *sphacelatus*) adults. After exposure for a month, Scathophagidae puparia (suggesting larvae had been present), Sphaeroceridae larvae and puparia, Hydrophilidae and Tipulidae larvae, and Staphylinidae adults and larvae were present. After 2-3 months, low numbers of *Aphodius* spp. larvae were found in and below the pats.

(c) Pats deposited in June:

Fresh pats contained Hydrophilidae, Staphylinidae and *Aphodius* spp. (A. *fimetarius* and A. *foetidus*) adults. After a month there was no evidence of any Scathophagidae activity, but large numbers of *Aphodius* spp. larvae were present, along with Chironomidae, Hydrophilidae, Sphaeroceridae and Tipulidae larvae, and Staphylinidae adults and larvae.

(d) Pats deposited in September:

Fresh pats were highly attractive to Hydrophilidae, Staphylinidae and *Aphodius* spp. (A. *contaminatus*, A. *rufipes* and A. *rufus*) adults, and also contained large numbers of Scathophagidae, Anthomyiidae and Sphaeroceridae larvae. After 2 months' exposure, large numbers of Psychodidae and Chironomidae larvae were found, along with small numbers of *Aphodius* spp. larvae.

DISCUSSION

From the results, it would appear that seasonality and ageing of the dung are very important in determining the composition of the dung fauna on Islay. This compares well with the results of previous studies (e.g. Hammer, 1941; Laurence, 1952; Landin, 1961; Putman, 1983).

The seasonal succession of taxa found during this study was also very similar to that found by the aforementioned authors. It is interesting to note that the lack of Scathophagidae larvae in pats deposited in midsummer has also been found previously (e.g. Parker, 1970; Gibbons, 1987), and appears to be due to adult mortality during periods of high temperature (Ward & Simmons, 1990).

From the point of view of the chough, it would appear that the best feeding opportunities in cow dung are presented (a) during the 'summer' months, when fresh dung contains large numbers of beetle adults and developing fly larvae, and (b) during late autumn, when pats deposited during the summer months are old enough for the large numbers of *Aphodius* spp. larvae present to have attained a reasonable size.

It is evident, however, that potential prey items are associated with cow dung, in any stage of decay, throughout most of the year. Only during the period from about October/November through to January, in a normal year would there appear to be a lack of suitably sized potential prey items in the dung. After this time the Tipulidae and Bibionidae larvae associated with the pats (see also Chapter 5) are large enough to be taken by the chough.

The practice of out-wintering cattle on Islay would therefore appear to be important to the chough, because it allows potential prey items, especially fly larvae, to develop in the dung as far into the winter as temperatures allow. In addition, the presence of fresh pats on pasture in the spring means that dung is available for colonisation as soon as the insects start to become active again.

It is interesting to note that during the winter of 1988/89, when temperatures on the island were well above the seasonal norm (see Chapter 3), Scathophagidae adults were active on fresh pats, and low numbers of larvae were susequently found in the dung, throughout this period.

Amano (1988) reported that the developmental temperature threshold for *Scathophaga stercoraria* (L.) larvae was between 2.8 and 3.3 °C in northern Japan. Also, adult activity was related to air temperature, with adults remaining active on pasture until the mean 5-daily air temperature declined to about 0 °C.

On this basis, it would be feasible for *S. stercoraria* to be active, in low numbers, on Islay throughout most winters. However, as Japanese flies may be physiologicaly different to British ones (Gibbons, 1987) the relevance of Amano's results to the situation on Islay is not clear.

CHAPTER SEVEN:
CHOUGH FAECAL ANALYSIS

INTRODUCTION

In Britain, a number of researchers (Bullock, 1980; Roberts, 1982; Warnes, 1982) have employed faecal analysis during the course of their investigations into the dietary requirements of the chough. To avoid confusion with the faeces of other birds, all used a single, fresh dropping as their basic sampling unit, and identified prey items from remains within the dropping. As there is considerable bias in such an approach, largely due to different rates of digestion of prey items, quantitative data were not included in the analyses of these studies. Instead, faeces collected at the same time of year were taken as belonging to a grouping, and the results were presented as the percentage frequency of occurrence of each prey item in the faeces of each grouping (e.g. 90% of the faeces collected in November 1980 at Coul, Islay contained earwig remains - from Warnes, 1982).

These studies certainly indicate the general diet of the chough in the areas concerned, but the lack of quantitative data means that the relative importance of a particular prey item at any time of year is difficult to determine. The main aim of this study was to address this problem by the use of alternative collection and analytical techniques.

On Islay, an individual chough, whether roosting communally (immatures throughout the year; some breeding birds in winter) or at the breeding site (most breeding birds in summer; some in winter), tends to use one particular roost site repeatedly (Monaghan, 1988b). Its faeces accumulate directly below this site, and it is possible to collect these accumulations at regular intervals. Samples (of a standard size) from these 'faecal mounds' should provide more accurate indications of the types and numbers of prey items taken within that period.

Use of this method on a large number of 'faecal mounds', accumulated at different times of the year, followed by comparison of the resulting data by multivariate methods, should provide a more comprehensive analysis of the chough's diet.

METHODS

Data collection

Two types of faeces were collected for analysis: adult, from 'faecal mounds' at roosting sites; and chick, in the form of discrete faecal sacs produced by the chicks in the nest. Chick faeces are usually removed from the nest by the adults and therefore do not accumulate. For the purpose of this study, they were considered to contain prey provided by the adults on the day of collection.

Two samples (each 3ml in volume) were taken from each collection of faeces, and each sample (hereafter referred to as a subsample) was given an identification code. The sites from which chough faeces were collected are shown in Table 7.1, and their approximate locations on Islay are shown in Fig. 7.1.

Each subsample was washed through a sieve (aperture width 0.32mm), and the associated taxa identified and counted under a binocular microscope. The presence of cereal grains and weed seeds was noted and their abundance estimated. The washings were also examined for the presence of earthworm chaetae. A total of 50 taxa were identified (Table 7.2).

TABLE 7.1. Sites from which chough faeces were collected for analysis. The site and subsample codes, type of faeces collected, and the period over which the faeces accumulated are shown. See text for further information.

SITES AND SUBSAMPLES	TYPE OF FAECES	PERIOD OVER WHICH FAECES ACCUMULATED
R35 A & B	ADULT	? - 2/11/86
W1 A & B	ADULT	? - 9/07/88
R71 A & B	ADULT	18/01/88 - 23/03/88
R71 C & D	ADULT	23/03/88 - 29/04/88
R71 E & F	ADULT	29/04/88 - 14/07/88
R71 G & H	ADULT	14/07/88 - 11/10/88
R71 I & J	ADULT	11/10/88 - 01/12/88
R71 K & L	ADULT	19/01/89 - 10/03/89
R71 M & N	ADULT	10/03/89 - 01/05/89
R71 O & P	ADULT	01/05/89 - 05/06/89
R71 Q & R	ADULT	05/06/89 - 19/07/89
E6 A & B	ADULT	? - 03/10/86
E6 C & D	CHICK	31/05/89
E19 A & B	CHICK	22/05/89
R25 A & B	CHICK	31/05/89
R5 A & B	CHICK	30/05/89
R67 A & B	CHICK	22/05/89
R7 A & B	CHICK	01/05/89
E13 A & B	CHICK	22/05/89
R1 A & B	ADULT	20/01/88 - 21/03/88
R1 C & D	ADULT	? - 30/04/89
R24 A & B	ADULT	02/11/86 - 28/11/86
R24 C & D	ADULT	14/12/86 - 12/02/87
E18 A & B	ADULT	02/11/86 - 28/11/86
E18 C & D	ADULT	13/12/86 - 12/02/87
R69 A & B	CHICK	30/05/89
R31 A & B	CHICK	30/05/89
E11 A & B	ADULT	20/01/88 - 22/03/88
R53 A & B	CHICK	05/06/89
E21 A & B	ADULT	? - 29/04/89

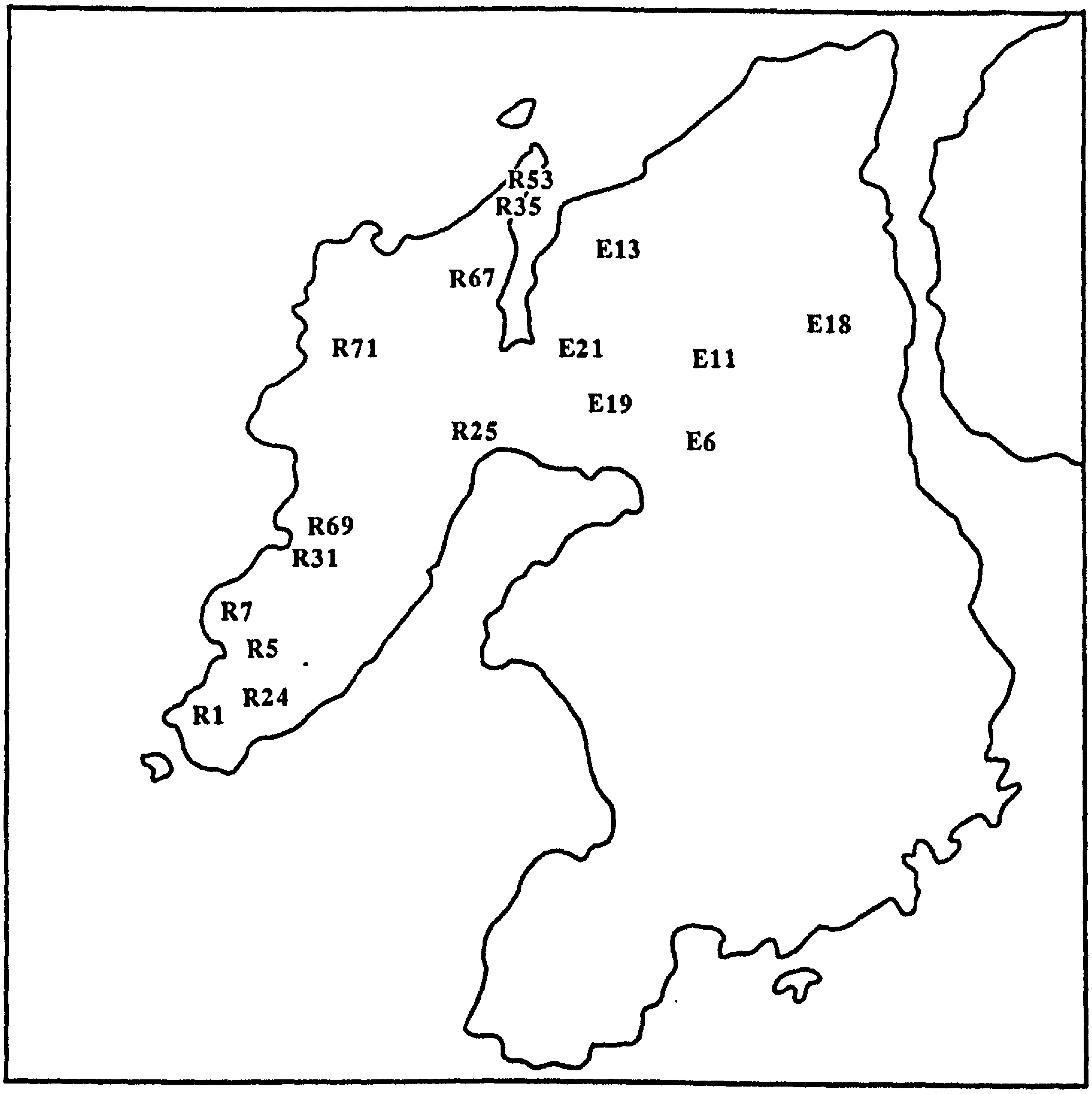


Fig. 7.1. Location on Islay of the sites from which chough faeces were collected. For reasons of security only the approximate positions are shown.

TABLE 7.2. Taxa identified in chough faeces. An 8-letter abbreviation and a code number are shown for each taxon.

COLEOPTERA		
Cantharidae larvae	CANTLARV	20
Carabidae adults	CARAADUL	21
" larvae	CARALARV	22
Curculionidae		
Philopedon plagiatus (Schaller) adults	PLAGADUL	34
Other weevil adults	WEEVADUL	50
Elateridae		
Agriotes spp. adults	AGRIADUL	1
Agriotes spp. larvae	AGRILARV	2
Athous spp. adults	ATHOADUL	15
Athous spp. larvae	ATHOLARV	16
Ctenicera cuprea (F.) adults	CCUPADUL	23
Ctenicera cuprea (F.) larvae	CCUPLARV	24
Geotrupidae		
Geotrupes spp. adults	GEOTADUL	28
Hydrophilidae		
Cercyon spp. adults	CERCADUL	25
Helophorus spp. adults	HELOADUL	29
Sphaeridium spp. adults	SPHAADUL	40
Scarabaeidae		
Aphodius ater (Degeer) adults	APHOATER	5
Aphodius contaminatus (Herbst) adults	APHOCONT	6
Aphodius depressus (Kugelann) adults	APHODEPR	7
Aphodius fimetarius (L.) adults	APHOFIME	8
Aphodius foetidus (Herbst) adults	APHOFOET	9
Aphodius fossor (L.) adults	APHOFOSS	10
Aphodius rufipes (L.) adults	APHORUFI	12
Aphodius rufus (Moll) adults	APHORUFU	13
Aphodius sphacelatus (Panzer) adults	APHOSPHA	14
Aphodius spp. larvae	APHOLARV	11
Serica brunnea (L.) adults	SERRBRUN	38
Silphidae adults	SILPADUL	39
Staphylinidae adults	STAPADUL	44
" larvae	STAPLARV	45
DIPTERA		
Anisopodidae larvae	ANISLARV	3
Bibionidae larvae	BIBILARV	17

Table 7.2 cont;

Calliphoridae larvae	CALILARV	18
" puparia	CALIPUPA	19
Muscidae		
Morellia spp. puparia	MOREPUPA	31
Polietes spp. larvae	POLILARV	35
Other Muscidae larvae	MUSCLARV	32
" " puparia	MUSCPUPA	33
Scathophagidae larvae	SCATLARV	36
" puparia	SCATPUPA	37
Sphaeroceridae larvae	SPHALARV	41
" puparia	SPHAPUPA	42
Tipulidae adults	TIPUADUL	46
" larvae	TIPULARV	47
" pupae	TIPUPUPA	48
OTHER		
Araneae - spiders	SPIDPRES	43
Cereal seed remains	CEREPRES	26
Dermaptera - *Forficula auricularia* L.	FORFAURI	27
Formicidae - ants	ANTSPRES	4
Lepidopteran larvae	LEPILARV	30
Weed seed remains	WEEDPRES	49

The minimum number of each taxon present in each subsample was calculated. Coleoptera adults and larvae were mainly identified from head capsules, mandibles and legs. Diptera larval and pupal stages were identified from posterior spiracles and mouthparts. Lepidoptera larvae were distinguished by their mandibles, Dermaptera by their cerci, and Formicidae by their head capsules. The presence of Tipulidae eggs was taken to imply that an adult had been consumed.

The final data set used in the analyses consisted of taxa abundances from 60 subsamples (see Appendix 4).

Classification and ordination

The 60 subsamples were classified by TWINSPAN (see Chapter 2), with the 'pseudo-species' function set to convert the abundance data into four classes: 1-4, 5-9, 10-24 and >24 individuals.

Taxa and subsamples were ordinated in three axes using DECORANA (see Chapter 2), without downweighting of rare taxa.

RESULTS

Classification

The classification of chough faecal content (and hence diet) on Islay, as interpreted from TWINSPAN end-groups, is given in Fig. 7.2, together with the indicator taxa at each division. There were no indicator taxa for end-groups A, E and G. Eight end-groups were recognized as representing distinct feeding strategies. The subsamples within each end-group are shown in Table 7.3, and the frequency of occurrence of each taxon within these end-groups is given in Table 7.4.

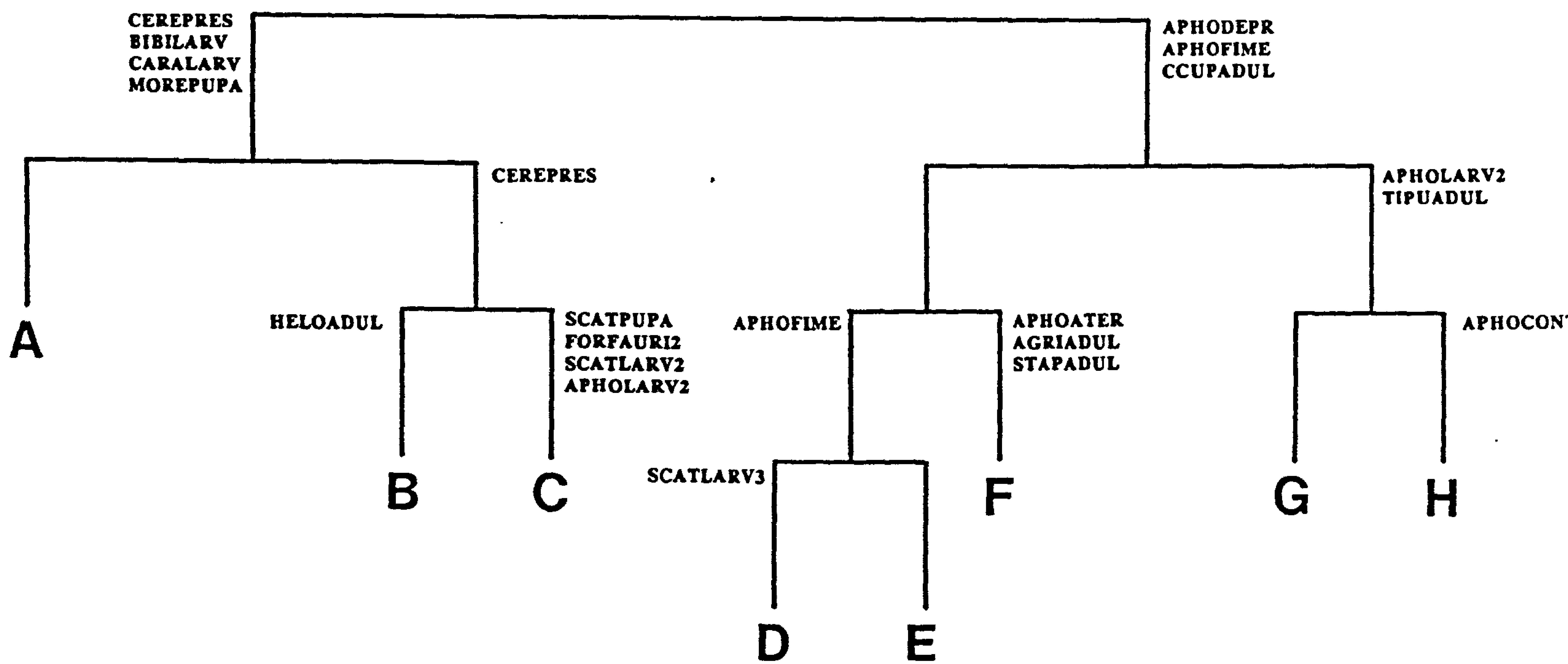


Fig. 7.2. Multivariate analysis of the chough faeces data set: dendrogram showing the eight end-groups interpreted from the TWINSPAN classification of the data. The indicator taxa at each division are shown (abbreviations as in Table 7.2), and the numbers indicate the 'pseudo-species' class where it is other than 1.

TABLE 7.3. Multivariate analysis of the chough faeces data set: end-groups, with associated sites and subsamples, interpreted from TWINSPAN analysis. See Table 7.1 and text for further information.

END-GROUP	SITES AND SUBSAMPLES							
A	W1A	W1B	R7A	R7B	E18C	E18D		
B	R71A	R71B	R71C	R71D	R71K	R71L	R71M	R71N
	R1A	R1B	R1C	R1D	R24C	R24D	E11A	E11B
	E21A	E21B						
C	R71G	R71H	R71I	R71J	R24A	R24B	E18A	E18B
D	R67A	R67B	E13A	E13B				
E	R25A	R25B	E19A	E19B	R69A	R69B	E6C	E6D
F	R71E	R71F	R71O	R71P	R71Q	R71R	R5A	R5B
	R31A	R31B						
G	R35A	R35B	R53A	R53B				
H	E6A	E6B						

TABLE 7.4. Multivariate analysis of the chough faeces data set: the frequency of occurrence of taxa within the TWINSPAN end-groups, where a taxon occurs in >20% of the subsamples in one of the end-groups (D=21-40%; C=41-60%; B=61-80%; A=81-100%). The taxa order is derived from the TWINSPAN analysis and the abbreviations are as shown in Table 7.2.

TAXA	TWINSPAN END-GROUP							
	A	B	C	D	E	F	G	H
BIBILARV	-	A	C	-	-	-	-	-
HELOADUL	D	C	-	-	-	-	-	-
CEREPRES	-	A	A	-	-	-	-	-
MOREPUPA	D	C	C	-	-	-	-	-
POLILARV	-	-	D	-	-	-	-	-
SCATPUPA	D	-	B	-	-	-	-	-
APHOSPHA	-	D	D	-	D	D	-	C
CARALARV	A	A	C	-	D	D	-	A
FORFAURI	A	B	A	C	-	C	B	C
ANISLARV	-	-	D	-	-	-	-	-
ANTSPRES	D	D	C	-	-	-	-	-
SPHAPUPA	D	-	-	-	-	-	-	-
SPIDPRES	C	-	-	-	-	-	-	-
APHOCONT	-	D	B	-	-	-	-	A
CARAADUL	C	A	A	B	D	C	B	A
WEEVADUL	D	C	D	-	-	D	D	-
LEPILARV	B	C	D	C	D	A	A	A
STAPADUL	C	D	D	-	-	B	D	-
TIPULARV	A	A	A	A	A	A	B	A
APHORUFI	-	-	D	-	-	D	D	A
SCATLARV	-	D	B	A	D	-	C	-
TIPUPUPA	D	-	D	-	B	-	-	A
APHOLARV	-	C	A	-	-	D	A	A
TIPUADUL	-	D	C	-	C	-	A	A
APHOFOET	-	-	-	-	-	-	C	-
APHOFOSS	-	-	-	-	-	-	C	-
GEOTADUL	-	D	D	-	C	C	B	A
AGRIADUL	B	-	-	-	D	B	-	-
CCUPLARV	-	-	-	-	-	D	C	-
PLAGADUL	C	-	C	A	D	B	B	-
SILPADUL	D	-	-	-	-	D	D	-
STAPLARV	B	D	C	B	B	C	D	-
APHOATER	-	-	-	-	-	B	D	-
CERCADUL	-	-	-	-	-	D	-	-
APHODEPR	-	-	-	A	A	B	B	A
CCUPADUL	-	-	-	A	B	C	-	-
SPHAADUL	-	-	-	A	-	-	-	C
APHOFIME	-	-	-	B	A	-	A	-
CALILARV	-	-	-	-	B	-	B	-
CALIPUPA	-	-	-	-	-	-	D	-
APHORUFU	-	-	-	-	-	-	C	-
ATHOADUL	-	-	-	-	-	-	D	-
SERRBRUN	-	-	-	-	-	-	C	-
WEEDPRES	-	-	-	-	-	-	C	A

Interpretation of the end-groups was based on knowledge of (1) the ecology of the taxa that occurred frequently within them, (2) the number of individuals of these taxa within the subsamples of an end-group, and (3) the areas from which the subsamples were collected. 'Site integrity' (see Chapter 2) was essential to ensure that the interpretation of the classification was meaningful. The end-groups were described as follows:

End-group A: 6 subsamples, collected from adults in south-west Scotland (July 1988), and from adults (February 1987) and chicks (May 1989) on Islay. Tipulidae larvae were abundant in all these subsamples. In addition, the chicks were provided with numbers of Sphaeroceridae larvae; and numbers of ants (south-west Scotland only), spiders (Islay only) and Carabidae larvae were taken by the adults. On the basis of their taxa compositions, these subsamples were 'under-represented' in the data set. They therefore proved difficult to classify within TWINSPAN, hence their position at one extreme of the classification.

End-group B: 18 subsamples, all from adults and covering the period December to April. Cereals, probably either gleaned from stubble fields or taken at cattle feeding stations, formed the staple diet at this time of year, with Bibionidae and Tipulidae larvae being taken in numbers from pastures as they became bigger, and presumably easier to find. Other insects uncovered while searching in pastures (e.g. Carabidae adults and larvae) were taken as the opportunities arose.

End-group C: 8 subsamples, all from adults and mainly collected between October and December. Cereals and insects obtained from feeding in dung were abundant in the diet at this time of year. Taxa taken in numbers included dung beetle (*Aphodius* spp.) larvae and adults, and Scathophagidae larvae and puparia. Earwigs also featured prominently during this period.

End-groups D and E contained subsamples collected from chicks between 22 and 31 May 1989.

End-group D: 4 subsamples from Ardnave, an area of coastal pasture heavily grazed by cattle and sheep. On the day of collection the chicks received large numbers of Scathophagidae larvae, *Philopedon plagiatus* adults (a weevil occurring mainly in sandy places), and Tipulidae larvae. Small numbers of dung-associated (*Aphodius* and *Sphaeridum* spp.) and surface-active (Elateridae and Carabidae) adult beetles were also provided.

End-group E: 8 subsamples from more inland areas. These chicks were provided with Calliphoridae larvae, probably obtained from carrion, and large numbers of Tipulidae larvae on the collection days. Small numbers of Staphylinidae larvae, and *Aphodius* spp. and Elateridae (*C. cuprea*) adults were also provided. This suggests that dung was largely unavailable and/or contained few taxa in these areas at this time.

End-group F: 10 coastal subsamples, collected from both adults and chicks between May and July. As in end-group D, Tipulidae larvae and *P. plagiatus* adults were abundant in these subsamples, but, as these areas are not so heavily grazed, fewer dung-associated insects (*Aphodius* spp. adults and larvae) were present. Also, being later in the year, a greater variety of surface-active insects were taken, including Lepidoptera larvae, and Elateridae (*Agriotes* spp.) and Staphylinidae adults.

End-group G: 4 subsamples collected from the Ardnave area - R35A and R35B from adults at the beginning of November 1986, and R80A and R80B from chicks at the beginning of June 1989. Although a variety of taxa were present in these subsamples, very high numbers of *Aphodius* spp. larvae and adults were found, indicating that dung-associated taxa were extremely important in this area at these times.

End-group H: 2 subsamples collected at the beginning of October 1986 from adults at an inland site. Weed seeds were taken in numbers from this area at this time, along with small numbers of *Aphodius contaminatus* adults and *Aphodius* spp. larvae.

Ordination

Fig. 7.3 shows the centroids of the end-groups interpreted from the TWINSPAN analysis plotted against the first 3 DECORANA axes, without downweighting of rare taxa. Their positions (with associated standard errors) and relative distances from one another are given in Table 7.5. The variance accounted for (based on eigenvalues of 0.707, 0.467 and 0.332) was 47, 31 and 22% for axes 1, 2 and 3 respectively.

Axis 1 appears to be related to seasonality, since the winter/spring subsamples (end-groups B and C) lie at one extreme, the summer/autumn subsamples (end-groups G and H) lie at the other, and the spring/summer subsamples (D, E and F) lie in between.

Axis 2 appears to be related to feeding strategy. The subsamples within which large numbers of dung-associated taxa were found had the lowest scores along axis 2, whilst those containing more surface-active taxa, or taxa not associated with dung, had the highest.

Axis 3 is possibly related to the location of the subsamples on the island. Coastal subsamples, with access to sandy pastures, had the lowest scores on this axis, whilst those occurring inland, or without access to sandy pasture, had the highest.

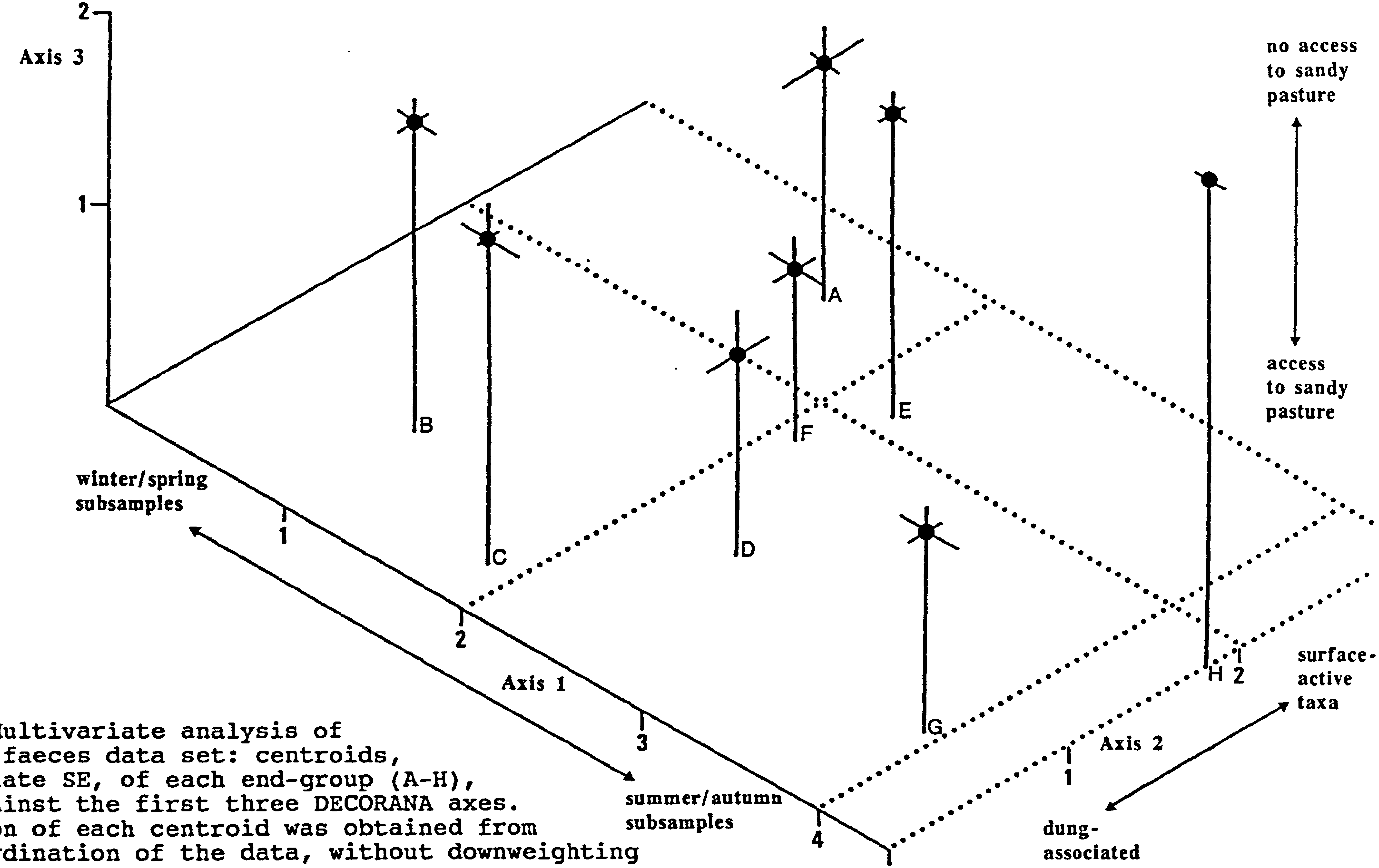


Fig. 7.3. Multivariate analysis of the chough faeces data set: centroids, with associate SE, of each end-group (A-H), plotted against the first three DECORANA axes. The position of each centroid was obtained from DECORANA ordination of the data, without downweighting of rare taxa.

TABLE 7.5. Multivariate analysis of the chough faeces data set: positions, with associated SE, on each DECORANA axis and distances between centroids of each TWINSPAN end-group. All positions and distances are in DECORANA axis units.

END-GROUP	POSITION			DISTANCE FROM END-GROUP						
AXIS:	1	2	3	B	C	D	E	F	G	H
A	148± 8	255±24	121±14	193	234	183	95	110	308	329
B	98±21	72± 8	154±12		96	161	191	166	297	371
C	183±17	27± 6	160±19			116	191	166	218	313
D	246± 2	102±17	97±23				125	80	148	260
E	227± 6	213± 6	153±10					81	225	237
F	211±14	173±10	85±16						209	284
G	390±17	66± 9	102± 9							196
H	439± 9	180± 1	254± 3							

From the calculated distances between end-groups (Table 7.5) it can be seen that end-groups B and C were close, as were end-groups D and F; E and F; and A and E. In all cases however, the standard errors of the mean subsample scores on each axis were small relative to the distances between centroids, indicating that the definitions of these end-groups were valid.

DISCUSSION

Interpretation is an important part of end-group analysis. Discussion points already raised may be summarised as follows:

the seasonal availability of prey items is the most important factor influencing chough diet throughout the year;

cereals are extremely important in the diet from October to April;

Tipulidae and Bibionidae larvae supplement cereals from January to April, and Tipulidae larvae are taken in large numbers until July;

where available, dung-associated insects are important components of the diet during spring (when young are in the nest), and late summer and autumn (supplementing cereal intake);

during the summer a greater variety of surface-active insects is exploited.

Warnes (1982) also investigated the diet of the chough on Islay, and concluded that *Aphodius* spp. adults and their larvae formed the staple diet throughout the year. It is clear, however, from the present study, that although *Aphodius* spp. are taken throughout the year, they only assume real dietary importance in spring (when adults are taken), and during late summer and autumn (when larvae are available in large numbers). Tipulidae larvae (spring only) and Scathophagidae larvae are also of great importance in the diet at these times.

Warnes also suggested that cereals (oats) were an important winter food source for flock-feeding birds, but not for pairs that remained on their breeding grounds. All the winter faeces used in the present study were collected from such pairs, and the importance of cereals in their diet has already been stated.

As in 1982, no evidence of earthworm remains were found in the chough faeces, and ants did not appear to be important prey items on Islay at any time of the year. It is interesting to note that ants were found in numbers in the faeces collected in mainland south-west Scotland.

The taxa taken in numbers by the chough at any particular time of year compares well with those taxa shown to be abundant on pasture at that time (see previous three chapters). Only fewer Carabidae adults appear to be taken than would be predicted from the numbers present as, for example, indicated by the use of pitfall traps (Chapter 4). These beetles possess chemical defence mechanisms (Dettner, 1987), which may make them distasteful to predators, and in addition, many may be nocturnal (Thiele, 1977) and therefore not readily available to the birds.

Paired chough are very territorial during the breeding season (Warnes, 1982). Although potential prey items may be abundant at a site during the spring and summer, if that site lies within a pair's breeding territory, then other chough within flying distance may not have access to it at this time.

The smallest prey items taken by chough on Islay were ants, at about 4-5 mm in length. It should be remembered that other potential prey items, such as Psychodidae larvae which are of this size or even smaller, may have been taken by the birds, but would have been too easily crushed to leave any recognizable remains in the faeces.

The presence of cattle on Islay would therefore appear to be of great importance to the continuing survival of the chough population there, (a) because of the invertebrates that colonise their dung, and (b) because the practice of out-wintering these cattle provides an important source of cereal foodstuffs at a time when few potential invertebrate prey items are available.

Finally, although the data used were 'noisy' (in that the faecal samples were collected over a number of years), interpretable classifications and ordinations of subsamples on taxa composition were obtained. The collection and analytical techniques described would therefore appear to provide an accurate and comprehensive assessment of the chough's dietary requirements on Islay throughout the year.

CHAPTER EIGHT:
THE EFFECT OF IVERMECTIN ON THE INVERTEBRATE FAUNA OF COW DUNG

INTRODUCTION

From the literature review (Chapter 2) it can be seen that at the start of this research, (a) fears were being expressed over the potential impact of ivermectin on the invertebrate fauna of dung, and (b) previous studies had implied that dung was an important source of food for the chough. Concern was expressed that ivermectin had the potential to affect the chough indirectly through alteration of its food supply. An experiment was therefore carried out to investigate the effects of ivermectin residues on the fauna, particularly potential chough prey items, associated with cattle dung.

No figures were available at that time regarding the maximum concentration of ivermectin in cow pats after treatment of cattle. Ivermectin was therefore added to the experimental dung at levels estimated to be close to the maximum concentrations possible after injection of cattle with the recommended standard dose of 200 mcg/kg body weight (taking the pharmacokinetics of the drug into consideration).

METHODS

Data collection

Fresh dung was collected from cattle at the Crichton Royal Farm, Dumfries and stored at 4 ^{o}C until required. This was done because, (a) these cattle had not been treated with 'Ivomec' and therefore their dung was known to be ivermectin-free; (b) collecting all the dung at the one time meant that the dung used throughout the experiment was of the same consistency; and (c) these cattle were housed and therefore the large quantity of dung required was easily collected. Prior to deposition on pasture the dung was formed into 1 kg pats and a solution of 'Ivomec' (containing 1% w/v ivermectin), in 5 ml water, was thoroughly mixed into each pat. Four treatment levels were used: 2, 1, 0.5 and 0 mg/kg ivermectin.

The pats were placed in stratified random block plots on pasture adjacent to fields with cattle at Auchincruive, Ayrshire. The pats within each plot were lifted after 15, 30, 45, 60 or 90 days exposure. Each plot contained three replicates of each treatment i.e. a total of 60 pats. When a pat was lifted, a sample (900 cm^3 - area 15 x 15 cm, depth 4 cm) of the soil below was also taken. Soil was sampled from the pat site even if the dung had degraded.

Invertebrates from both dung and soil were obtained by hand-sorting and heat-extraction, and transferred to 70% alcohol for later identification. The study concentrated on the differences between the experimental pats with regard to the numbers and types of Diptera and Coleoptera present. The numbers of earthworms were also noted, but nematodes, mites and springtails were not examined.

A plot of pats was exposed on each of the following dates: 5 May, 19 June, 8 August, and 17 September 1988 (Table 8.1). Appendix 6 gives the treatment details for each pat, and includes the amount of temperature, rainfall and sunshine to which each pat was exposed while on the pasture.

Taxa were identified using the standard keys referred to in previous chapters. A total of 65 taxa (Table 8.2) were identified from dung and soil. The invertebrates extracted from the dung and the soil will be considered

TABLE 8.1. Experimental cow pats - exposure date, length of exposure and initial treatment (presence/absence ivermectin). The soil sample taken from below a pat was given the same code number. See text for further information.

DATE EXPOSED	DAYS OF EXPOSURE	EXPERIMENTAL COW PAT CODE NUMBERS: TREATED	EXPERIMENTAL COW PAT CODE NUMBERS: CONTROLS
5 MAY	15	001 - 009	010 - 012
	30	013 - 021	022 - 024
	45	025 - 033	034 - 036
	60	037 - 045	046 - 048
	90	049 - 057	058 - 060
19 JUNE	15	061 - 069	070 - 072
	30	073 - 081	082 - 084
	45	085 - 093	094 - 096
	60	097 - 105	106 - 108
	90	109 - 117	118 - 120
3 AUGUST	15	121 - 129	130 - 132
	30	133 - 141	142 - 144
	45	145 - 153	154 - 156
	60	157 - 165	166 - 168
	90	169 - 177	178 - 180
17 SEPTEMBER	15	181 - 189	190 - 192
	30	No samples taken at this time	
	45	193 - 201	202 - 204
	60	205 - 213	214 - 216
	90	217 - 225	226 - 228

TABLE 8.2. Taxa identified from the dung and the soil beneath the experimental cow pats. An abbreviation (6-8 letters) and a code number are shown for each taxon.

COLEOPTERA			
CARABIDAE			
Carabidae larvae	CARABL	33	
Clivina fossor (L.) adults	CLAVFOSA	58	
Nebria brevicollis (Fab.) adults	NEBRBREA	60	
Pterostichus strenuus (Panzer) adults	PTERSTRA	59	
Trechus spp. adults	TRECHUSA	61	
CRYPTOPHAGIDAE adults	CRYPTOA	55	
CURCULIONIDAE			
Apion spp. adults	APIONA	57	
Sitona spp. adults	SITONAA	56	
Sitona spp. larvae	SITONAL	34	
Sitona spp. pupae	SITONAP	62	
HYDROPHILIDAE			
Cercyon atomarius (Fab.) adults	CERCATOA	36	
C. haemorrhoidalis (Fab.) adults	CERCHAEA	40	
C. lateralis (Marsham) adults	CERCLATA	37	
C. lugubris (Olivier) adults	CERCLUGA	39	
C. melanocephalus (L.) adults	CERCMELA	35	
C. pygmaeus (Illiger) adults	CERCPYGA	38	
C. unipunctatus (L.) adults	CERCUNIA	41	
Cercyon spp. larvae	CERCYONL	29	
Cryptopleurum minutum (Fab.) adults	CRYPMINA	42	/n
Helophorus ~~*aequaticus*~~ (L.) adults	HELOAEQA	47	aequalis
Helophorus spp. adults	HELOSPPA	46	
Megasternum obscurum (Marsham) adults	MEGAOBSA	43	
Sphaeridium bipustulatum Fab. adults	SPHABIPA	45	
S. scarabaeoides (L.) adults	SPHASCAA	44	
Sphaeridium spp. larvae	SPHAERL	30	
PTILIIDAE adults	PTILIDA	54	
SCARABAEIDAE			
Aphodius ater (Degeer) adults	APHOATEA	50	
A. depressus (Kugelann) adults	APHODEPA	51	
Aphodius spp. larvae	APHODIL	31	
A. fimetarius (L.) adults	APHOFIMA	48	
A. prodromus (Brahm) adults	APHOPROA	49	
A. rufipes (L.)	APHORUFA	52	
STAPHYLINIDAE			
Staphylinidae adults	STAPHA	53	
" larvae	STAPHL	32	
DIPTERA			
ANISOPODIDAE larvae	ANISOPOL	05	
BIBIONIDAE larvae	BIBIONL	20	
CECIDOMYIIDAE larvae	CECIDOL	17	

Table 8.2 cont:

CERATOPOGONIDAE		
Culicoides spp. larvae	CULICOL	08
Forcipomyia spp. larvae	FORCIPOL	09
CHIRONOMIDAE		
Chironomidae larvae	CHIRONOL	06
Chironomidae/Ceratopogonidae pupae	MIDGEP	27
DOLICHOPODIDAE larvae	DOLICHOL	21
EMPIDIDAE larvae	EMPIDL	22
FANNIIDAE		
Fannia spp. larvae	FANNIAL	16
LONCHOPTERIDAE larvae	LONCHOPL	18
MUSCIDAE		
Hydrotaea spp. larvae	HYDROTAL	12
Muscina spp. larvae	MUSCINAL	13
Morellia spp. larvae	MORELIAL	14
Polietes lardaria (Fab.) larvae	POLILARL	15
Muscidae larvae (unknown)	MUSCIDUL	11
PSYCHODIDAE		
Psychodidae larvae	PSYCHOL	01
" pupae	PSYCHOP	23
SCATHOPHAGIDAE		
Scathophagidae larvae	SCATOL	03
" puparia	SCATOP	25
SCIARIDAE		
Sciaridae larvae	SCIARIDL	10
" pupae	SCIARIDP	28
SEPSIDAE		
Sepsidae larvae	SEPSIDL	02
" puparia	SEPSIDP	24
SPHAEROCERIDAE		
Sphaeroceridae larvae	SPHAEROL	04
" puparia	SPHAEROP	26
STRATIOMYIDAE larvae	STRATIOL	07
TIPULIDAE larvae	TIPULIDL	19
OTHER		
Araneae - Spiders	SPIDERS	64
Dermaptera - *Forficula auricularia* L.	FORFAURI	65
Oligochaeta - Earthworms	EARTHWS	63

separately.

(a) Dung

Appendix 5 shows the taxa abundances in each of the experimental pats. To avoid undue distortion, pats containing less than 3 taxa were not included in the data set for analysis. Ninety-four of the original 228 pats in the study were therefore excluded - 73 had no dung visible on the day of sampling and 21 contained < 3 taxa. These pats are considered in the section on dung degradation.

The final data set therefore contained abundance information on the taxa from 134 pats.

(b) Soil

Appendix 7 contains the taxa abundances in each of the soil samples taken from below the experimental pats. As with the dung, samples containing less than three taxa were not included in the data set used in the analyses.

The final data set therefore contained abundance information on the taxa in the soil samples from beneath 57 pats.

Classification and ordination

(a) Dung

The 134 pats were classified by TWINSPAN (see Chapter 2), with the 'pseudo-species' function set to convert the abundance data into four classes: 1-4, 5-9, 10-24 and >24 individuals.

Taxa and pats were ordinated in three axes using DECORANA (see Chapter 2), without downweighting of rare taxa.

In addition, CANOCO (see Chapter 2) was used with a combination of the taxa and environmental data (Appendix 6) to give a bi-plot indicating the most important factors affecting taxa distribution.

(b) Soil

The 57 soil samples were classified using TWINSPAN, with the 'pseudo-species' function set to convert the abundance data into 4 classes: 1-4, 5-9, 10-24 and >24 individuals.

Taxa and soil samples were ordinated in three axes using DECORANA, without downweighting of rare taxa.

RESULTS

(a) Dung

Classification

The classification of the dung data set is given in Fig. 8.1, together with the indicator taxa at each division. Eight end-groups were recognized as representing distinct taxa assemblages. The pats within each end-group are shown in Table 8.3, and the percentage belonging to each of the categories in Table 8.1 is shown in Fig. 8.2. As few differences were detected between the three levels of ivermectin applied, the pats were simply regarded as either treated or controls (see Section (c) on dosage response). The frequency of occurrence of each taxon within the end-groups is given in Table 8.4.

Exposure date (whether early season - May, June; or late season - August, September), length of exposure (15 days compared to 30+ days) and treatment (presence/absence of ivermectin) all appear to interact in determining the separation of the pats. The end-groups were described as

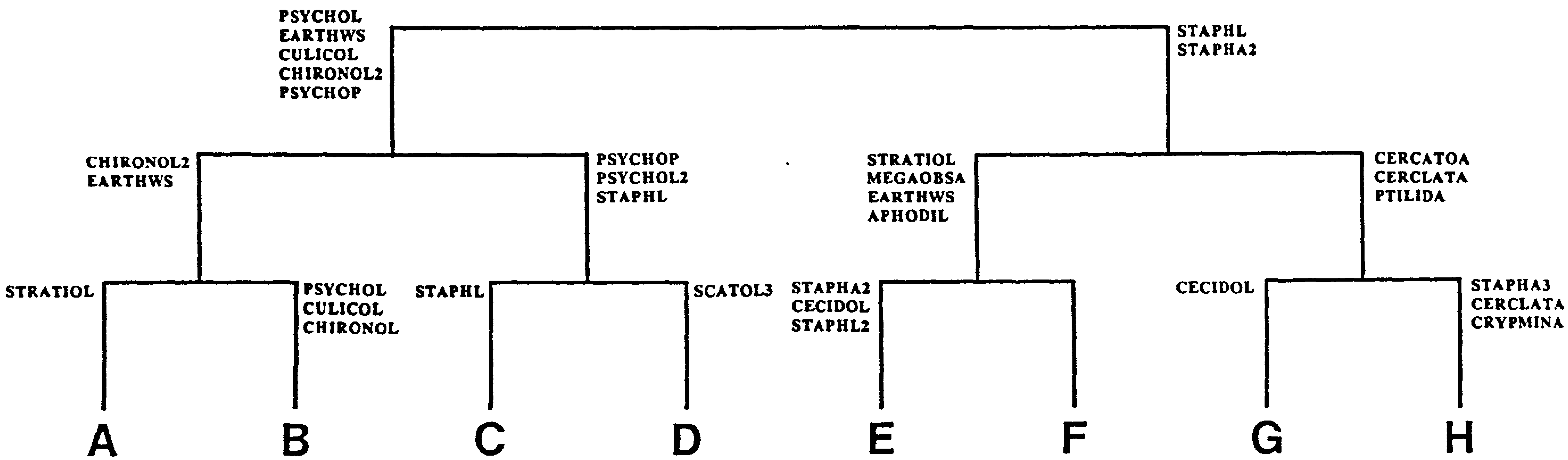


Fig. 8.1. Multivariate analysis of the dung data set: dendrogram showing the eight end-groups interpreted from the TWINSPAN classification of the abundance data. The indicator taxa at each division are shown (abbreviations as in Table 8.2), and the numbers indicate the 'pseudo-species' class where it is other than 1.

TABLE 8.3. Multivariate analysis of the dung data set: end-groups, with associated experimental cow pats, interpreted from TWINSPAN analysis of the abundance data. See Table 8.1 and text for further information.

END-GROUP	EXPERIMENTAL COW PATS
A	075 076 081 086 087 089 091 211
B	133 134 135 139 140 142 143 145 146 147 150 151 154 189 193 194 195 196 197 198 199 200 201 202 203 205 206 207 208 210 212 214 215
C	010 011 012 022 023 024 070 082 083 084 121 126 127 129 130 131 132 144 204 216
D	128 187 190 191 192
E	035 061 064 065 066 067 068 069 071 072 125
F	037 046 055 073 074 077 078 079 080 085 088 090 092 093
G	013 014 015 017 018 019 020 025 026 027 028 029 030 031 032 033 036 038 039 040 041 042 043 044 045 047 186
H	001 002 003 004 005 006 007 008 009 016 021 062 063 122 123 124

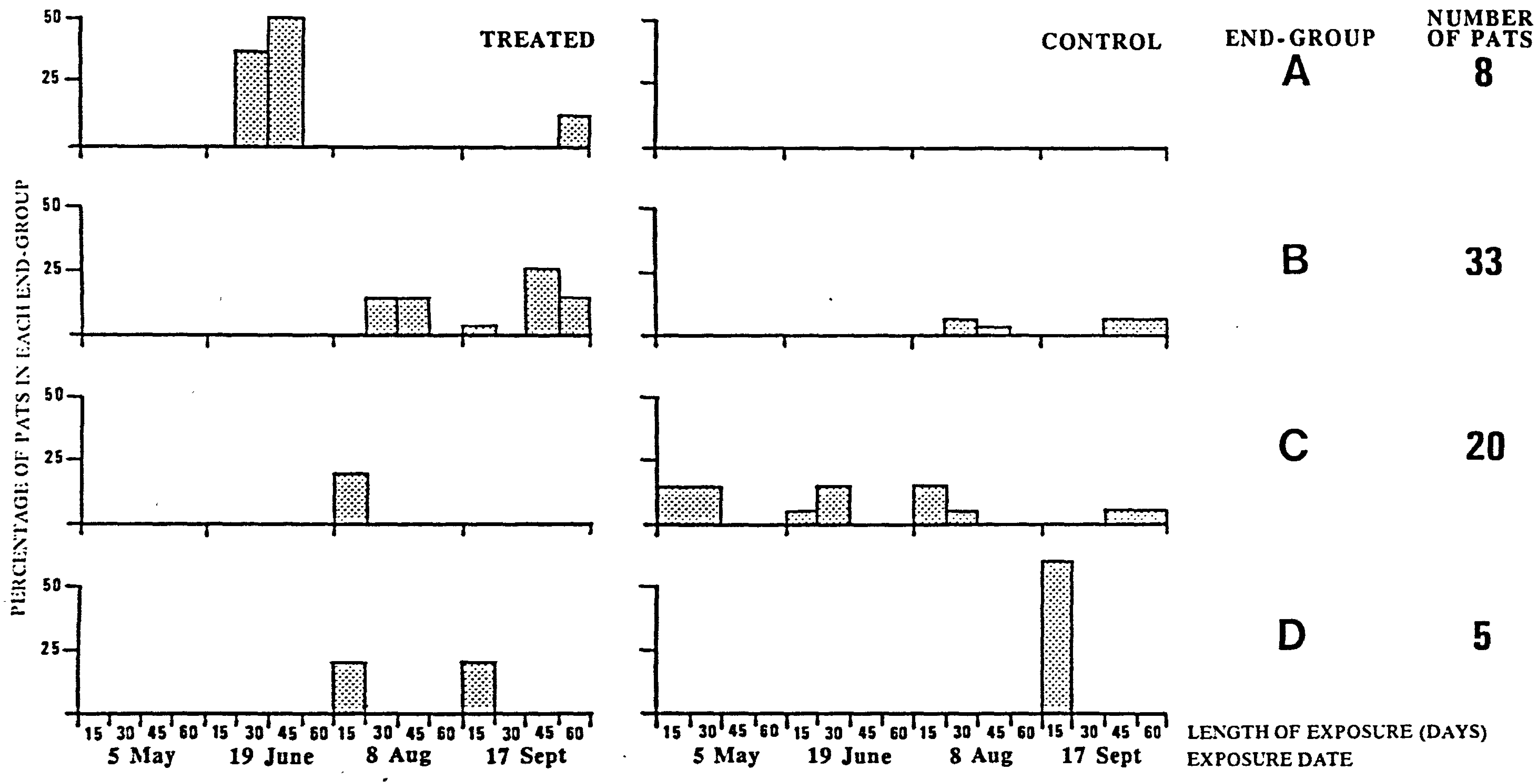


Fig. 8.2. Multivariate analysis of the dung data set: percentages of pats in each TWINSPAN end-group belonging to each of the categories shown - i.e. with regard to exposure date, length of exposure and whether or not ivermectin was initially applied to the pats (see Table 8.1).

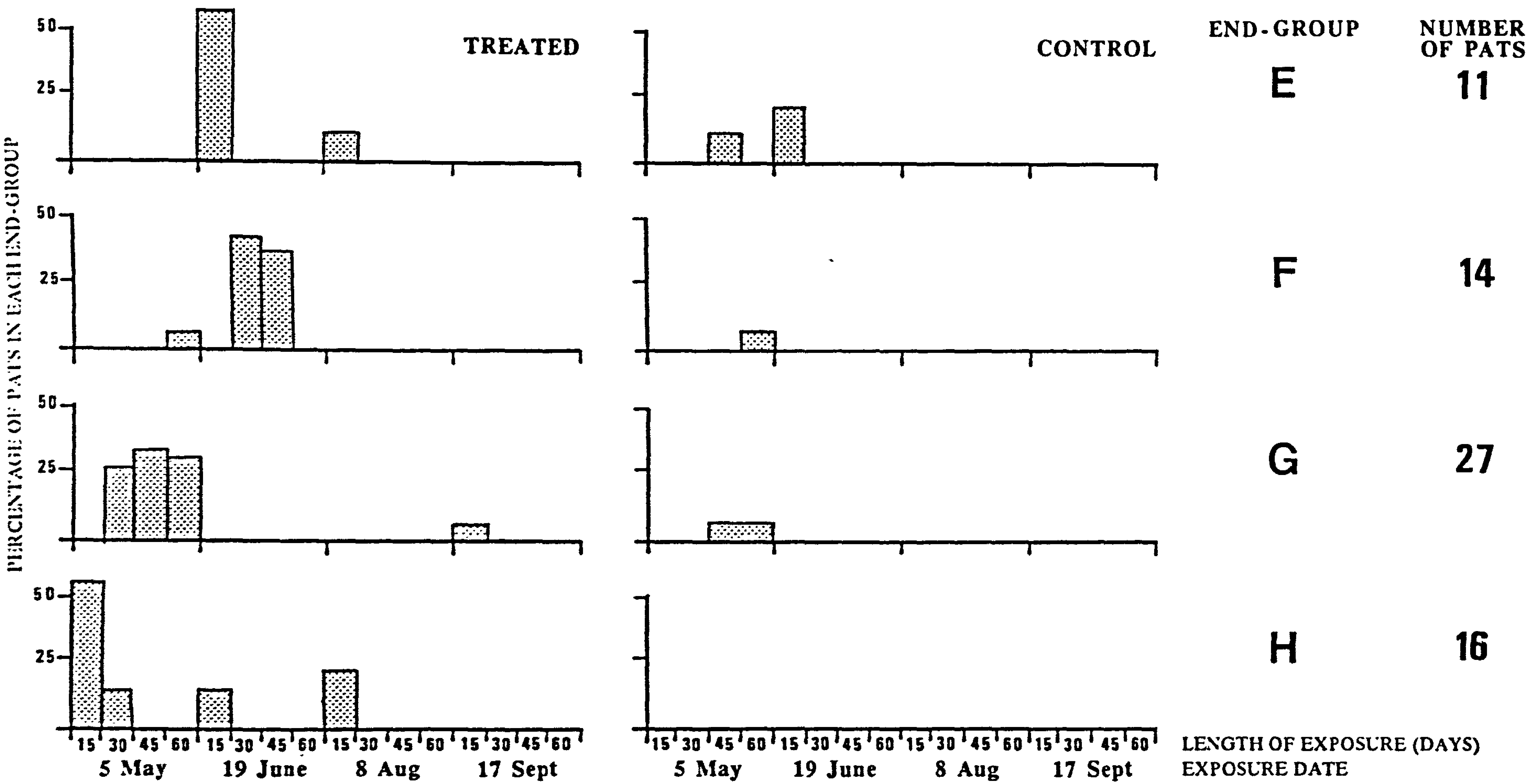


Fig. 8.2 cont. Multivariate analysis of the dung data set: percentages of pats in each TWINSPAN end-group belonging to each of the categories shown - i.e. with regard to exposure date, length of exposure and whether or not ivermectin was initially applied to the pats (see Table 8.1).

TABLE 8.4. Multivariate analysis of the dung data set: the frequency of occurrence of taxa within the end-groups derived from TWINSPAN analysis of the abundance data, where a taxon occurs in >20% of the experimental cow pats in one of the end-groups (D=21-40%; C=41-60%; B=61-80%; A=81-100%). The taxa order is derived from the TWINSPAN analysis and the abbreviations are as shown in Table 8.2.

TAXA	END-GROUP							
	A	B	C	D	E	F	G	H
TIPULIDL	-	D	-	-	-	-	-	-
CHIRONOL	D	A	B	-	-	C	C	D
HELOSPPA	D	C	D	-	-	-	-	-
EARTHWS	B	A	D	-	-	C	-	-
CULICOL	-	A	C	-	-	-	-	-
MUSCIDUL	-	-	-	D	-	-	-	-
HELOAEQA	-	-	-	D	-	-	-	-
SEPSIDL	-	-	B	-	D	-	-	-
SPHAEROL	-	-	C	-	-	-	-	-
ANISOPOL	-	-	D	-	-	-	-	-
POLILARL	-	-	-	D	-	-	-	-
PSYCHOP	-	D	A	C	D	-	-	-
PSYCHOL	-	B	A	A	C	-	-	-
SCATOL	-	-	-	A	-	-	-	D
CERCYONL	-	C	B	-	C	-	-	-
APHODIL	-	-	C	-	D	-	-	-
SCIARIDL	-	D	D	-	C	-	-	-
APHOPROA	-	-	-	D	-	-	-	-
STRATIOL	A	-	D	-	A	B	-	-
MEGAOBSA	C	D	D	D	C	B	-	D
LONCHOPL	-	-	-	-	-	D	-	-
CERCLATA	-	-	C	-	-	-	-	A
CRYPMINA	-	-	D	-	-	-	-	B
CECIDOL	-	-	D	-	A	-	B	-
STAPHL	D	-	A	-	A	A	A	B
CERCMELA	-	-	-	-	-	-	D	D
STAPHA	D	D	A	A	A	B	B	A
CERCHAEA	-	-	-	D	-	-	-	-
PTILIDA	-	-	C	-	-	D	B	C
CRYPTOA	-	-	-	-	-	-	-	C
CERCATOA	-	-	-	-	-	-	C	C
SPIDERS	-	-	-	-	-	-	D	-

follows:

End-group A: a group of treated pats, the majority of which were put on pasture in June and sampled 30 and 45 days later. Stratiomyidae larvae and earthworms were prevalent in these pats.

End-group B: a large collection of pats, all of which were exposed in August or September. Most of these pats had been treated with ivermectin and were sampled 30+ days after exposure. A small number of control pats, lifted after 30+ days, were also included in this group. Earthworms and Chironomidae, Ceratopogonidae and Psychodidae larvae occurred in these pats.

End-group C: a group consisting mainly of control pats collected 15 and 30 days after exposure. These pats contained the most diverse fauna e.g. Staphylinidae adults and larvae, Psychodidae larvae and pupae, Chironomidae and Sepsidae larvae, and *Cercyon* spp. larvae.

End-group D: a small group of pats, the majority of which were controls placed on pasture in September, all sampled after 15 days exposure. Psychodidae and Scathophagidae larvae, and Staphylinidae adults were prevalent in these 'late season' pats.

End-group E: a collection of mainly treated pats, the majority exposed in June and sampled 15 days later. Stratiomyidae and Cecidomyiidae larvae, and Staphylinidae adults and larvae were prevalent in these pats.

End-group F: a group very similar to A, containing treated pats exposed in June and sampled 30+ days later. Although Staphylinidae adults and larvae were more prevalent in these pats, on the whole, the taxa present were very similar to those found in end-group A.

End-group G: a large group mainly consisting of treated pats placed on pasture in May and sampled 30+ days after exposure. Staphylinidae adults and larvae, Cecidomyiidae larvae and Ptiliidae adults were active in these pats.

End-group H: a group largely similar to G, with the exception that the majority of these pats were sampled after 15 days exposure. Staphylinidae adults and larvae were prevalent in these pats, along with *Cercyon lateralis* and *Cryptopleurum minutum* adults.

Ordination by DECORANA

Fig. 8.3 shows the centroids of the end-groups interpreted from the TWINSPAN analysis plotted against the first three DECORANA axes. Their positions (with associated standard errors) and relative distances from one another are given in Table 8.5. The variance accounted for (based on eigenvalues of 0.925, 0.512 and 0.289) was 54, 30 and 16% for axes 1, 2 and 3 respectively.

As with the TWINSPAN classification, the ordination of the end-groups in each axis appears to be determined by a combination of exposure date, length of exposure and ivermectin presence/absence.

Axis 1 appears to be largely related to the length of exposure on pasture, as the 15 day exposure pats either occur at one extreme (end-group D), or occur towards that end of the axis when compared with similar pats lifted after 30+ days (e.g those in end-group H compared to those in G).

Axis 2 appears to be related to seasonality, i.e. the date of exposure, as the pats exposed in May and June (e.g. those in end-groups E, F, G and H) lie towards one extreme of this axis, while those exposed in August and September (e.g. in B, C and D) lie towards the other.

Axis 3 appears to be related to presence/absence of

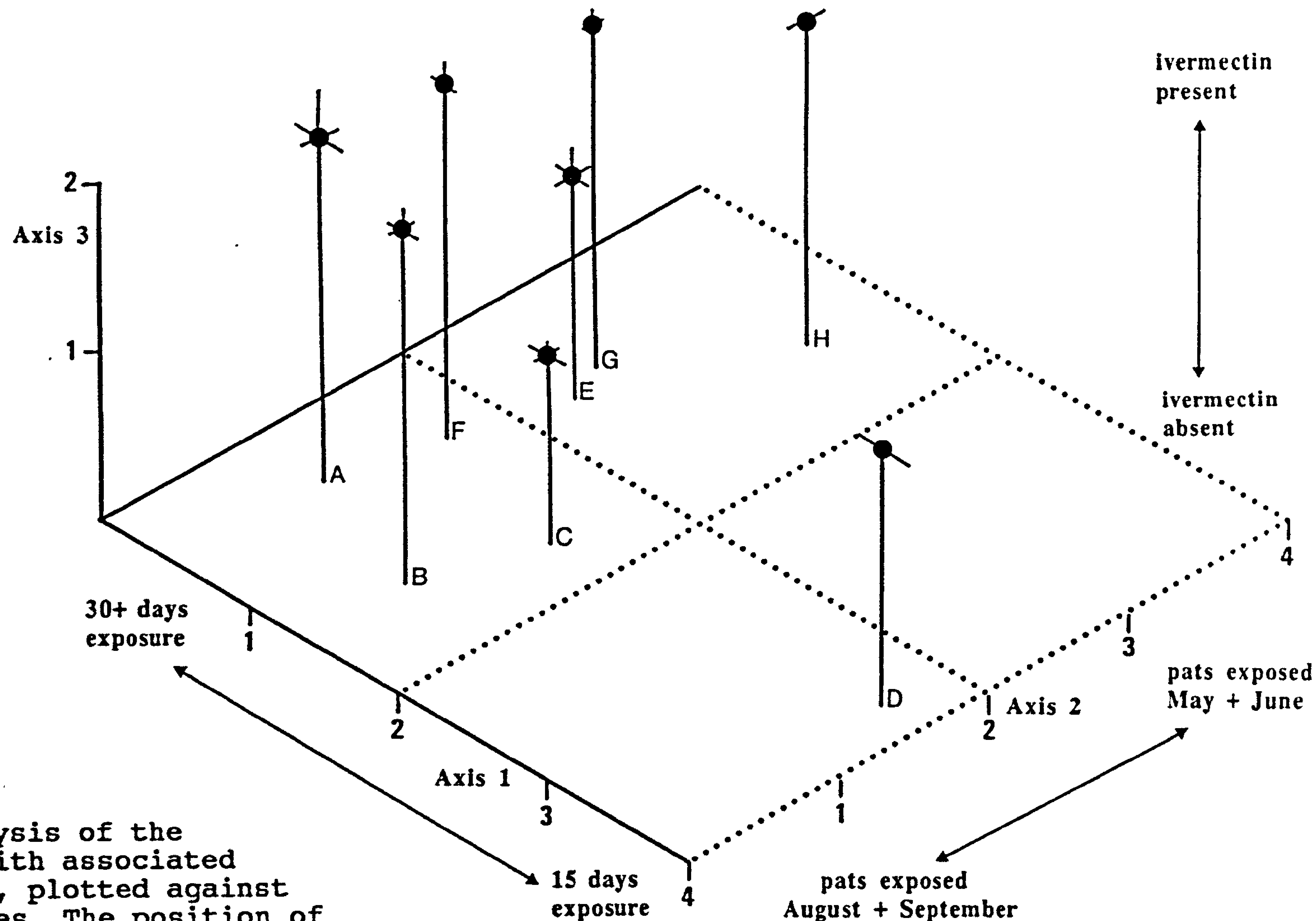


Fig. 8.3. Multivariate analysis of the dung data set: centroids, with associated SE, of each end-group (A-H), plotted against the first three DECORANA axes. The position of each centroid was obtained from DECORANA ordination of the abundance data, without downweighting of rare taxa.

TABLE 8.5. Multivariate analysis of the dung data set: position, with associated SE, on each DECORANA axis and distances between centroids of each end-group interpreted from TWINSPAN analysis of the abundance data. All positions are in DECORANA axis units.

END-GROUP	POSITION			DISTANCE FROM END-GROUP						
	Axis: 1	2	3	B	C	D	E	F	G	H
A	51 ± 17	98 ± 12	203 ± 26	94	149	322	154	66	163	258
B	138 ± 8	64 ± 8	210 ± 15		124	253	192	122	208	280
C	162 ± 10	137 ± 9	112 ± 7			213	125	142	175	222
D	370 ± 18	151 ± 5	157 ± 4				298	310	322	310
E	84 ± 10	232 ± 13	134 ± 16					107	69	132
F	65 ± 7	162 ± 14	213 ± 12						100	194
G	70 ± 3	260 ± 7	196 ± 5							102
H	129 ± 6	343 ± 12	189 ± 3							

TABLE 8.6. Multivariate analysis of the dung data set: correlation coefficients between environmental variables in the CANOCO analysis. See text for further information.

	19 JUNE	8 AUG	17 SEPT	REPNO	EXPOTIME	IVERLEVL	ACCTEMP	ACCRAIN	ACCSUN
5 MAY	-0.167	-0.322	-0.391	-0.055	-0.216	-0.068	-0.269	-0.539	0.452
19 JUNE		-0.230	-0.280	-0.043	-0.149	-0.176	-0.074	-0.248	-0.094
8 AUGUST			-0.541	-0.125	-0.019	-0.059	0.162	0.341	-0.147
17 SEPTEMBER				0.189	0.284	0.221	0.108	0.266	-0.164
REPNO					0.050	-0.077	-0.002	0.012	-0.008
EXPOTIME						-0.065	0.968	0.871	0.699
IVERLEVL							-0.104	0.005	-0.202
ACCTEMP								0.905	0.690
ACCRAIN									0.363

TABLE 8.7. Multivariate analysis of the dung data set: Inter set correlation coefficients of environmental variables with CANOCO axes. See text for further information.

ENVIRONMENTAL VARIABLES	AXIS 1	AXIS 2
5 MAY	0.250	0.065
19 JUNE	0.326	0.640
8 AUGUST	0.188	-0.290
REPNO	-0.016	0.026
EXPOTIME	0.426	-0.509
IVERLEVL	-0.359	-0.370

ivermectin, since the control pats occur at the lower end of this axis, and the treated pats lie at the other.

From the calculated distances between end-groups (Table 8.5) it can be seen that end-groups A and F were very close, as were end-groups E and G. For end-groups A and F, the standard errors of the mean pat scores on each axis were large compared to the distances between centroids. This would suggest, as reported in the TWINSPAN analysis, that these groups were similar, and should probably have been treated as one group. However, the fact that they were treated as two separate groups did not affect the final interpretation of the ordination. For the remaining end-groups, including E and G, the standard errors of the mean pat scores on each axis were small relative to the distance between centroids, indicating that the definitions of these end-groups were valid.

Ordination by CANOCO

It can be seen from the correlation coefficients between environmental variables (Table. 8.6) that the measurements of accumulated temperature, rainfall and sunshine were all highly correlated with length of exposure on pasture. The three former environmental variables were therefore removed from the analysis to avoid distortion of the ordination.

CANOCO ordination axes 1 and 2 (with eigenvalues of 0.719 and 0.457) together accounted for 64.5% of the variation in the analysis. The correlation coefficients between the remaining environmental variables and these ordination axes are shown in Table 8.7.

CANOCO bi-plots showing the relationships of the environmental variables to the distribution of the taxa and the pats in the TWINSPAN end-groups are given in Figs. 8.4 and 8.5, respectively. Note that only the taxa occurring

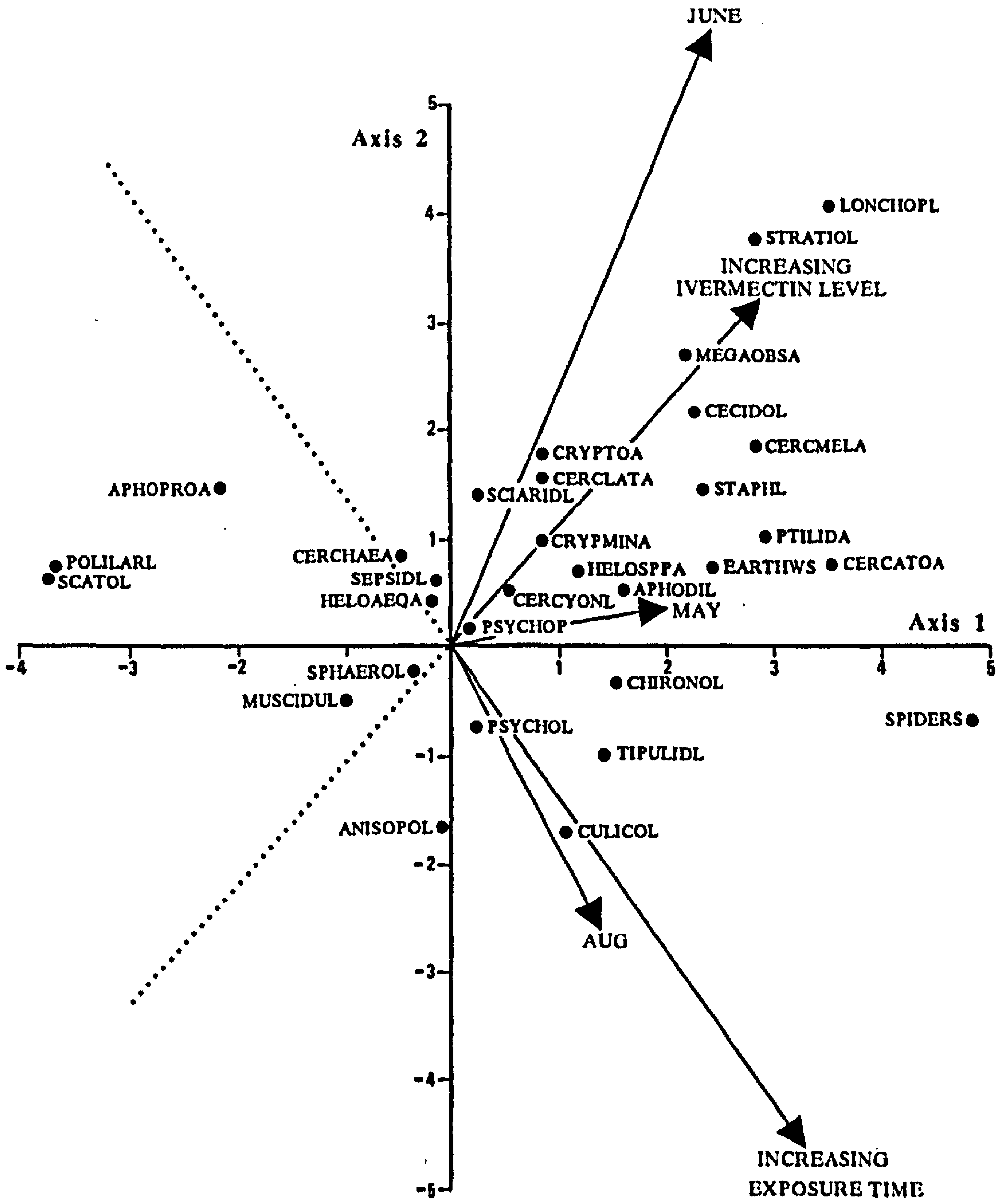


Fig. 8.4. Multivariate analysis of the dung data set: CANOCO bi-plot (axis 1 by axis 2) showing the distribution of the taxa in the abundance data set, and the amount of variation explained by each of the environmental variables, as shown by the length of the arrows. To reduce the complexity of the bi-plot, only the positions of those taxa occurring in Table 8.4 are shown.

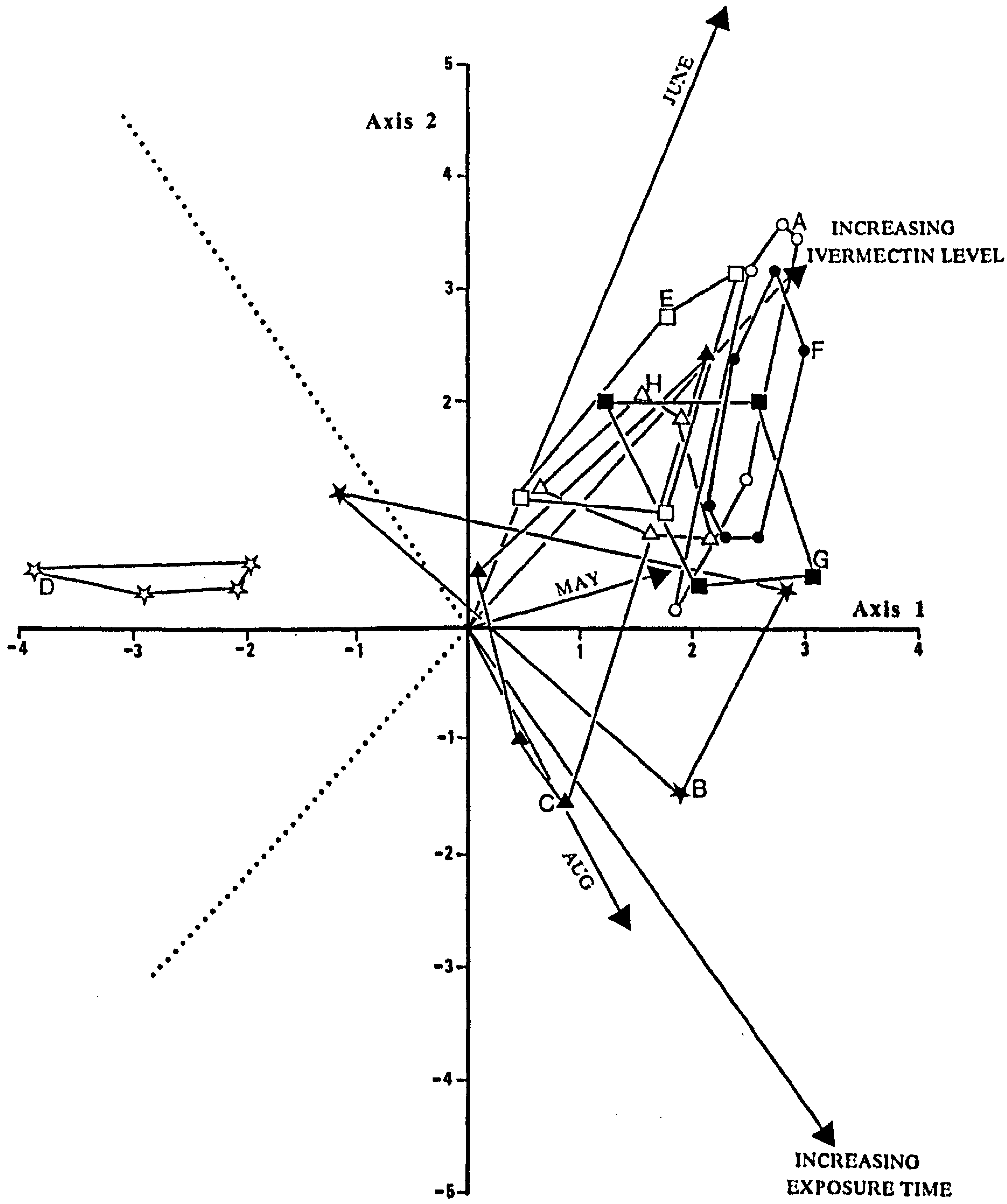


Fig. 8.5. Multivariate analysis of the dung data set: CANOCO bi-plot (axis 1 by axis 2) showing the distribution of the the experimental cow pats in the eight end-groups (A-H) interpreted from the TWINSPAN analysis of the abundance data, and the amount of variation explained by each of the environmental variables, as shown by the length of the arrows. Polygons enclose the space containing all the pats in each end-group.

in Table 8.4 are included in Fig. 8.4.

The environmental variables are shown as arrows, the relative lengths of which indicate their importance in the analysis. As with the DECORANA ordination plot, it can be seen that a combination of date of exposure, length of exposure and ivermectin treatment level determined the ordination of the taxa and pats in both axes.

(b) Soil

Classification

The classification of the soil data set is given in Fig. 8.6. No indicator taxa were provided by TWINSPAN for any of the divisions. Nevertheless, five end-groups were recognized as representing distinct taxa assemblages. The soil samples within each end-group are shown in Table 8.8, and the percentage belonging to each of the categories in Table 8.1 are shown in Fig. 8.7. The frequency of occurrence of each taxon within the end-groups is given in Table 8.9. The end-groups were described as follows:

End-group A: a group of samples mainly from beneath control pats placed on pasture in May. Staphylinidae adults and larvae were prevalent. Scathophagidae and Sphaeroceridae puparia, and Sepsidae and *Cercyon* spp. larvae were characteristic taxa found in these samples.

End-group B: a collection of samples, the majority of which were collected from below pats that were exposed in June and lifted 15 days later. Earthworms, and Staphylinidae adults and larvae were active in these samples.

End-group C: contained samples mainly collected from beneath treated pats exposed in May and sampled 15 days later. Tipulidae larvae and earthworms were prevalent under these pats.

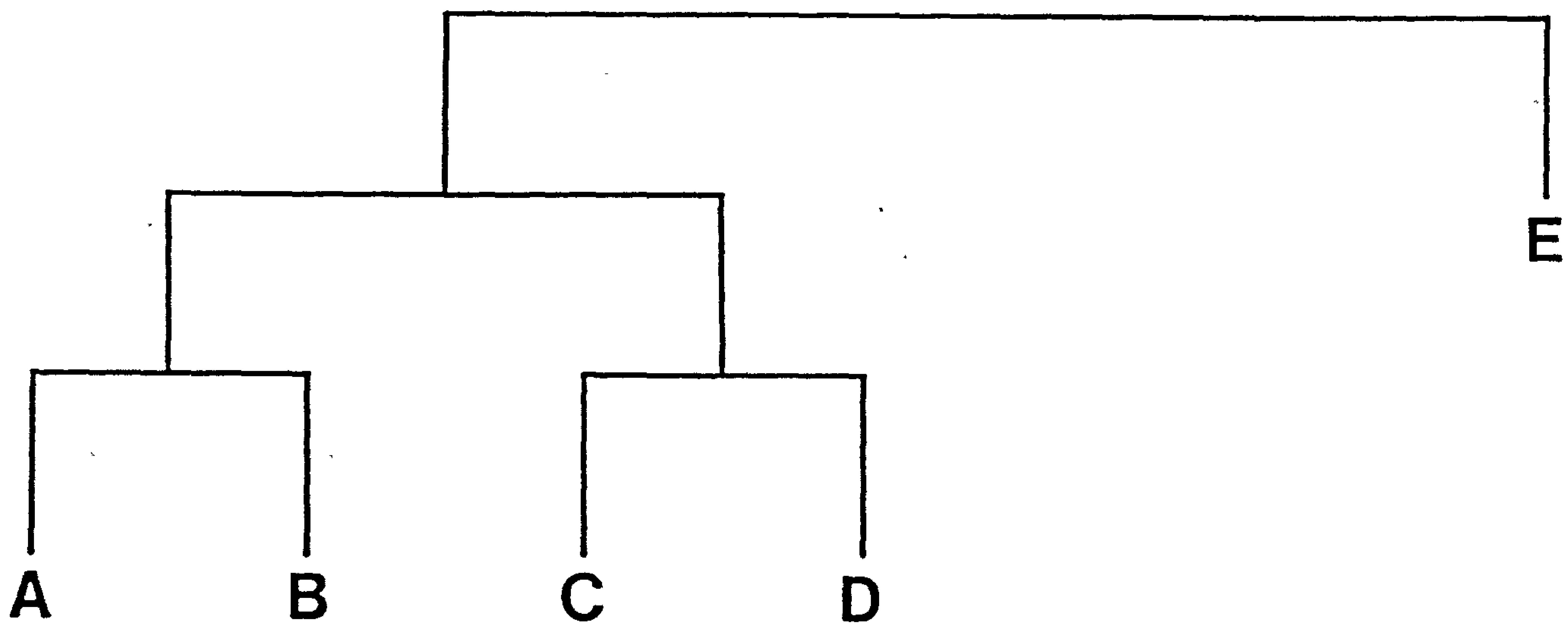


Fig. 8.6. Multivariate analysis of the soil data set: dendrogram showing the five end-groups interpreted from the TWINSPAN classification of the abundance data.

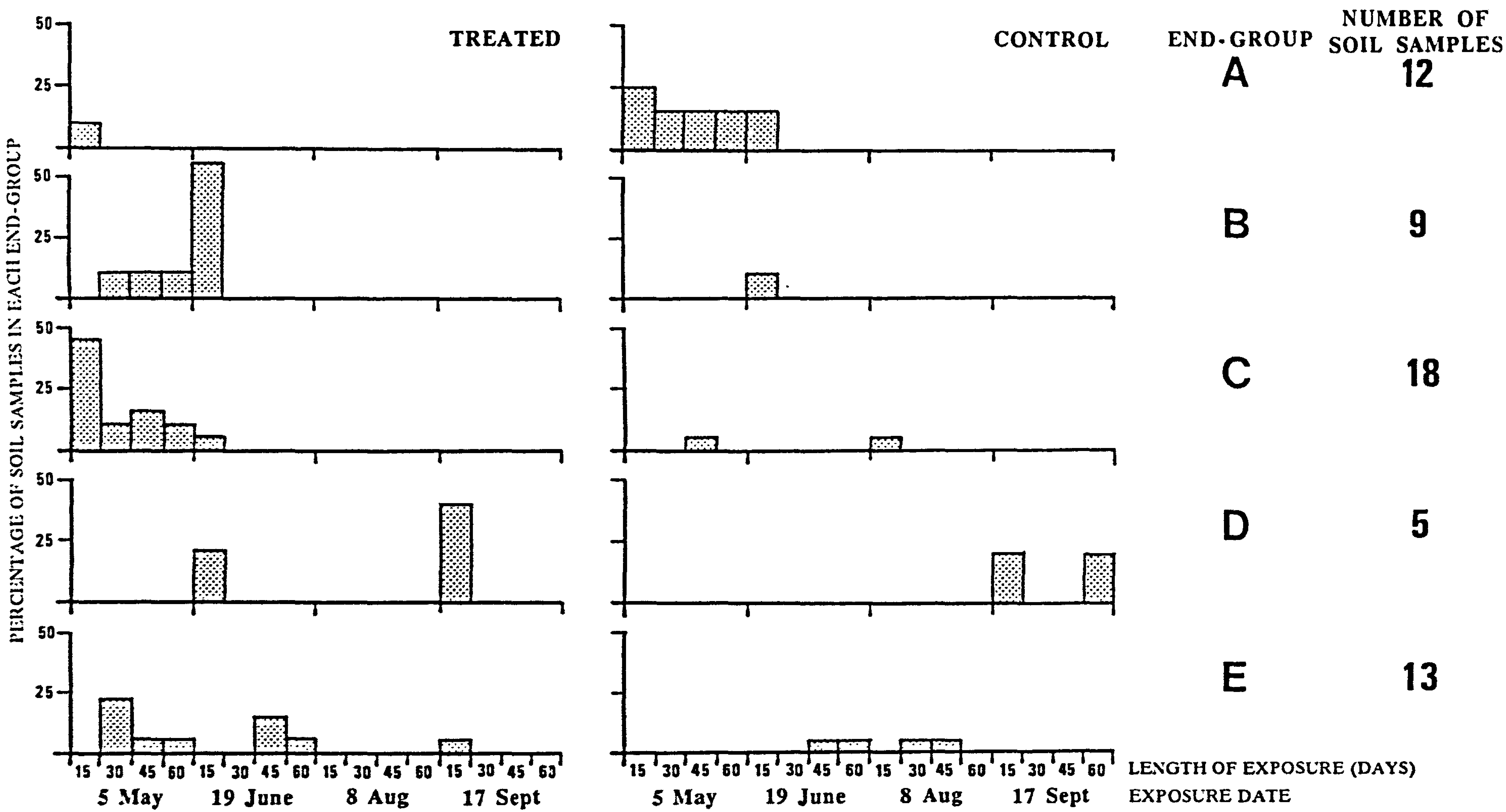


Fig. 8.7. Multivariate analysis of the soil data set: percentages of soil samples in each TWINSPAN end-group belonging to each of the categories shown - i.e. with regard to exposure date, length of exposure and whether or not ivermectin was initially applied to the pats from below which the soil samples were taken (see Table 8.1).

TABLE 8.8. Multivariate analysis of the soil data set: end-groups, with associated soil samples from below experimental cow pats, interpreted from the TWINSPAN analysis of the abundance data. See Table 8.1 and text for further information.

END-GROUP	SOIL SAMPLES
A	009 010 011 012 023 024 034 036 047 048 071 072
B	021 027 045 062 065 066 067 068 070
C	001 002 003 004 005 006 007 008 013 016 030 032 033 035 043 044 063 130
D	064 185 186 191 215
E	014 015 020 026 039 089 093 094 103 108 143 154 188

TABLE 8.9. Multivariate analysis of the soil data set: frequency of occurrence of taxa within the end-groups derived from TWINSPAN analysis of the abundance data, where a taxon occurs in >20% of the soil samples, from below the experimental cow pats, in one of the end-groups (D=21-40%; C=41-60%; B=61-80%; A=81-100%). The taxa order is derived from the TWINSPAN analysis and the abbreviations are as shown in Table 8.2.

	END-GROUP				
TAXA	A	B	C	D	E
STAPHL	B	B	C	-	D
BIBIONL	-	D	-	-	-
APHORUFA	-	D	-	-	-
SPIDERS	-	D	-	-	-
SEPSIDP	D	D	-	-	-
SEPSIDL	C	-	-	-	-
SPHAEROP	D	-	-	-	-
CERCYONL	B	-	-	-	-
PTILIDA	D	-	-	-	-
SCATOP	B	-	-	-	-
SITONAL	-	-	-	C	-
APHOPROA	-	-	-	C	-
CERCMELA	-	-	D	-	-
CERCATOA	-	-	C	-	-
TIPULIDL	C	-	B	-	-
CERCLATA	D	-	C	-	-
STAPHA	A	A	C	B	C
MEGAOBSA	-	D	-	-	-
EARTHWS	C	B	B	B	A
STRATIOL	-	-	-	-	D
CLAVFOSA	-	-	-	-	D

End-group D: a small number of samples taken from beneath pats placed on pasture in September. Earthworms and Staphylinidae adults were among the few taxa present in these samples.

End-group E: another group of samples containg relatively few taxa. These were mostly from under pats exposed in May and June and lifted 30+ days later. Only earthworms were found in all of these samples.

Ordination

Fig. 8.8 shows the centroids of the end-groups interpreted from the TWINSPAN analysis plotted against the first three DECORANA axes. Their positions (with associated standard errors) and relative distances from one another are given in Table 8.10. The variance accounted for (based on eigenvalues of 0.780, 0.659 and 0.434) was 42, 35 and 23% for axes 1, 2 and 3, respectively.

As with the dung data set, the ordination of the end-groups in each axis appears to be related to a combination of date of exposure, length of exposure and ivermectin presence/absence.

Axis 1 appears to be most related to length of exposure on pasture, since the samples taken from under pats exposed for 30+ days occur towards one extreme of the axis, whereas those from beneath pats sampled after 15 days lie towards the other.

Axis 2 appears to be largely related to ivermectin presence or absence, as the samples from beneath control pats occur towards the lower end of this axis compared to similar samples from beneath treated pats.

Axis 3 appears to be related to seasonality, as samples from beneath pats exposed in May lie at one end of this axis, while those from pats exposed later in the year lie at the other.

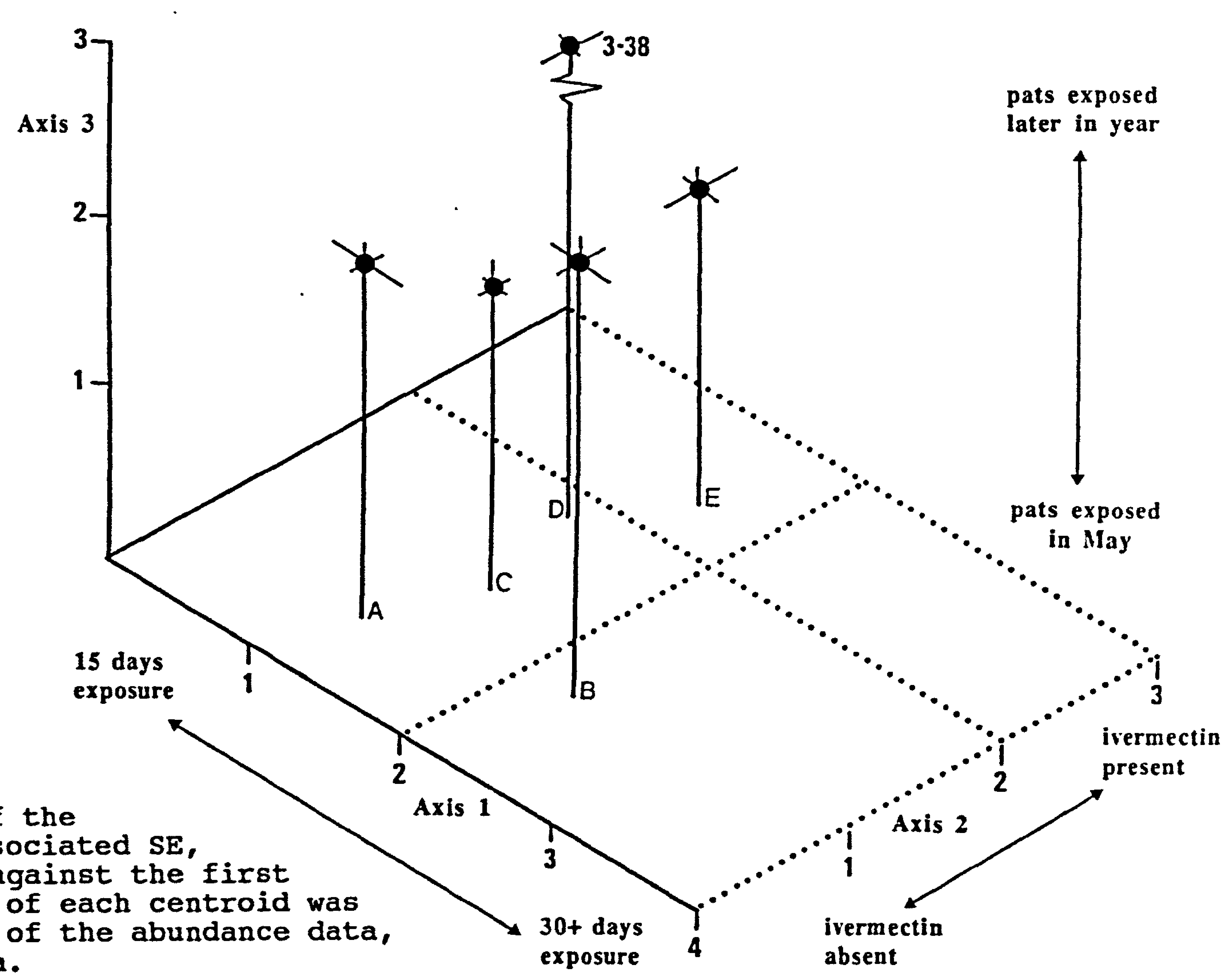


Fig. 8.8. Multivariate analysis of the soil data set: centroids, with associated SE, of each end-group (A-E), plotted against the first three DECORANA axes. The position of each centroid was obtained from DECORANA ordination of the abundance data, without downweighting of rare taxa.

TABLE 8.10. Multivariate analysis of the soil data set: position, with associated SE, on each DECORANA axis and distances between centroids of each end-group interpreted from TWINSPAN analysis of the abundance data. All positions are in DECORANA axis units.

END-GROUP	POSITION			DISTANCE FROM END-GROUP			
	Axis: 1	2	3	B	C	D	E
A	117±25	51±9	208±12	125	77	182	188
B	231±21	76±13	254±13		128	169	184
C	140±8	116±10	174±16			176	118
D	126±8	178±21	338±19				166
E	161±10	232±23	185±9				

The relative distances of the end-groups from one another (Table 8.10) suggest that end-groups A and C were similar i.e. those mainly containing samples from underneath pats exposed in May. However, the standard errors of the mean sample scores on axis 2 are small, relative to the distance between centroids, suggesting that the definition of these end-groups was valid.

(c) Dosage response

Although primarily designed to investigate the invertebrate fauna of the dung, the experiment also yielded some information on the responses of individual taxa to the different amounts of ivermectin used. It should be borne in mind, however, that any observed differences in response could also be due to the ivermectin affecting the numbers of other taxa, e.g. potential prey, present within the pat.

As mentioned earlier, few differences were detected between the three levels of ivermectin applied. Fig 8.9 shows the mean numbers (± SE) of 5 taxa (Psychodidae larvae and pupae; Sepsidae, Scathophagidae and *Cercyon* spp. larvae) in some of the experimental pats. It can be seen that, irrespective of the initial level applied, ivermectin had a pronounced effect on the numbers of these taxa found. This effect was probably indirect on the predacious *Cercyon* spp. larvae, but direct on the remaining, saprophagous, taxa.

Fig. 8.10 shows the mean numbers (± SE) of earthworms in the soil samples taken from below the pats exposed in August. Although it is clear that the numbers found depended on the length of exposure of the pats, no differences were detected between the levels of ivermectin applied.

The mean numbers (± SE) of Stratiomyidae and Chironomidae larvae found in some of the experimental pats are shown in Fig. 8.11. Both these taxa appear to exhibit a

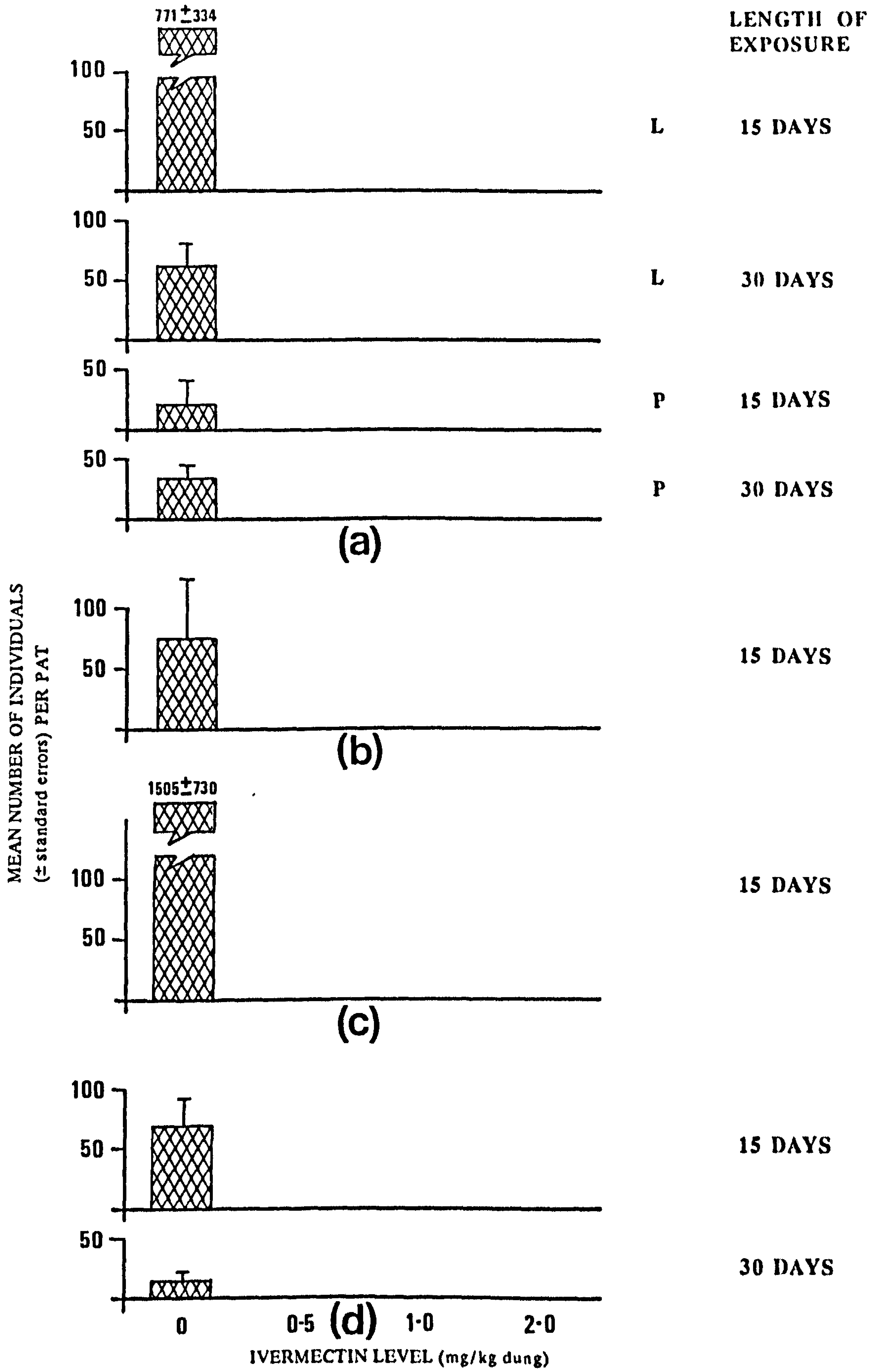


Fig. 8.9. Mean number of individuals (± SE) per pat after exposure of the pats on pasture for the length of time shown: (a) Psychodidae larvae (L) and pupae (P) in pats exposed 5 May; (b) Sepsidae larvae in pats exposed 19 June; (c) Scathophagidae larvae in pats exposed 17 Sept; and (d) *Cercyon* spp. larvae in pats exposed 5 May.

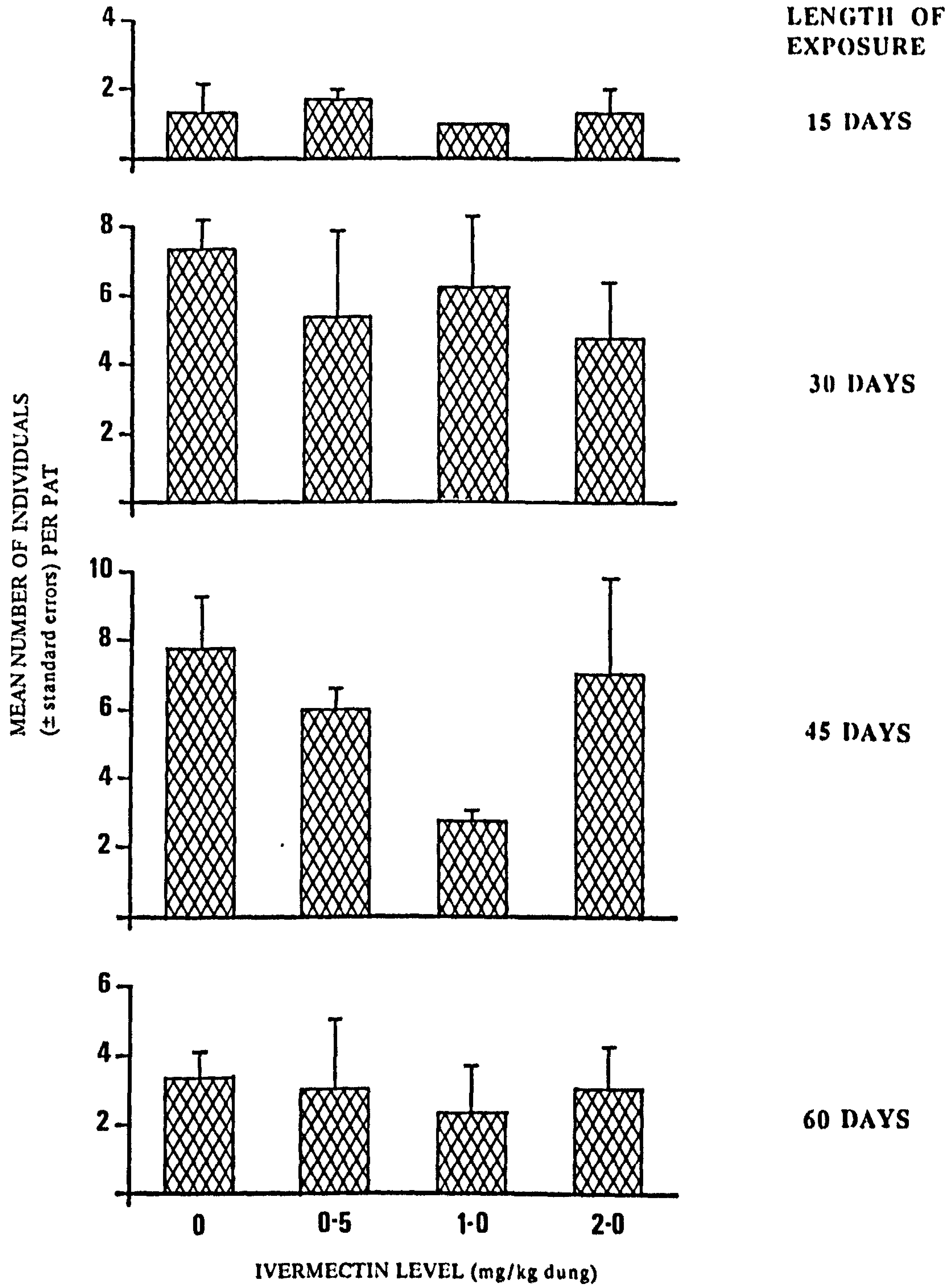


Fig. 8.10. Mean numbers (± SE) of earthworms in the soil samples taken from below the pats exposed on 3 August, after exposure of the pats on pasture for the length of time shown.

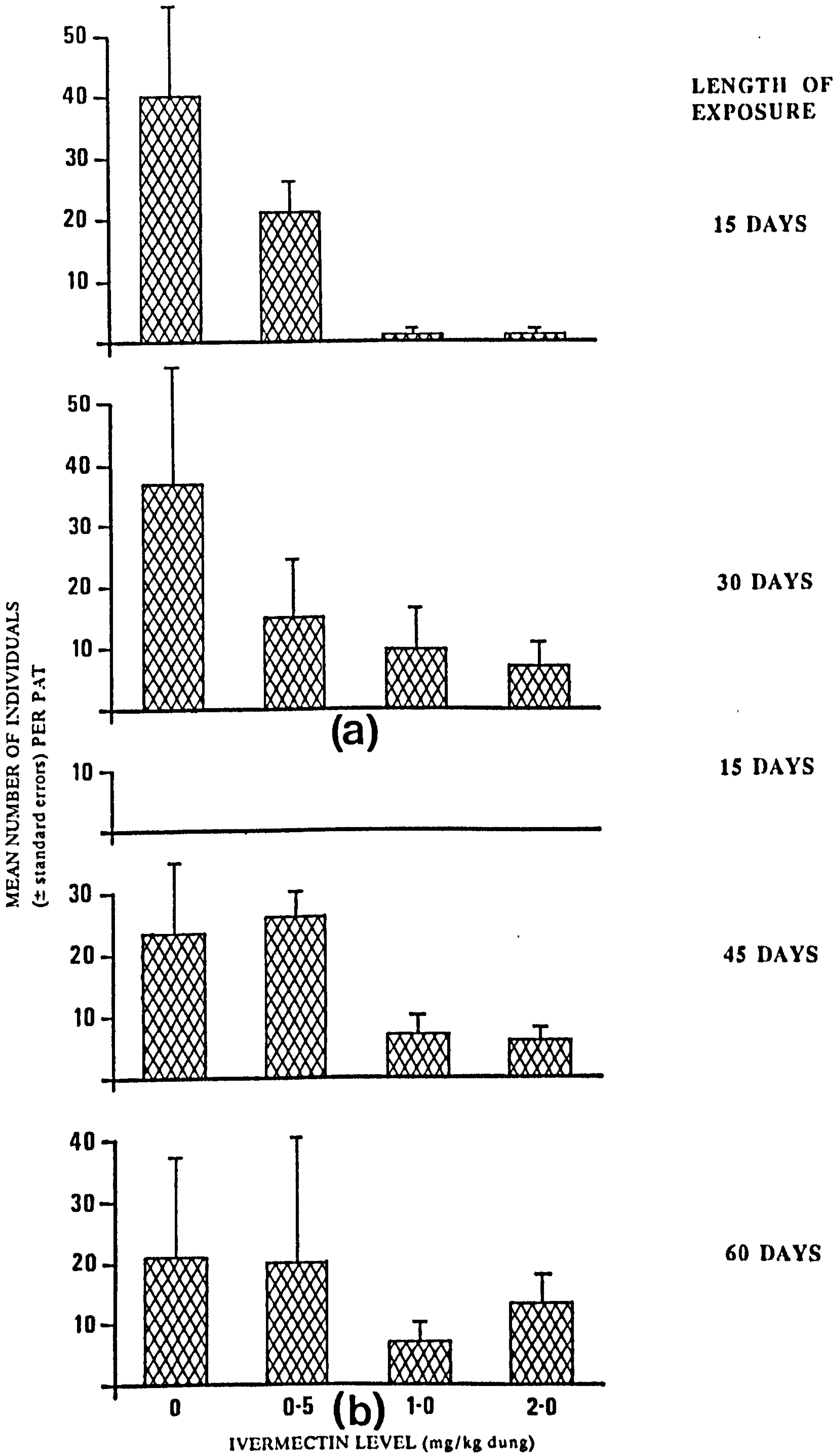


Fig. 8.11. Mean numbers of individuals (± SE) per pat after exposure of the pats on pasture for the length of time shown: (a) Stratiomyidae larvae in pats exposed 19 June; and (b) Chironomidae larvae in pats exposed 17 Sept.

dosage response to ivermectin. With regard to the numbers of Stratiomyidae larvae found after 15 days exposure, there was a marked difference between the pats initially treated with 0.5 mg/kg ivermectin and those treated with the higher levels. Chironomidae larvae showed a similar response after 45 days exposure. Ivermectin in dung would therefore appear to have an adverse effect on Stratiomyidae larvae at a concentration $\leq$ 0.5 mg/kg, and on Chironomidae larvae at a concentration of between 0.5 - 1.0 mg/kg.

In addition, throughout the duration of the experiment some taxa were only extracted in numbers from the control pats i.e. either from the dung or the soil beneath - these were Chironomidae/Ceratopogonidae pupae, Muscidae larvae, and Sepsidae, Sphaeroceridae and Scathophagidae larvae and puparia.

(d) Degradation of dung

The experiment also provided some information on the seasonal degradation rates of the dung. Fig. 8.12 shows the percentage of pats in each of the plots with dung visible on the day of sampling. It can be readily seen that the pats exposed in June and August degraded faster than those exposed in either May or September.

Also, in June the ivermectin-treated pats degraded significantly slower than the control pats: an exact probability test showed there was a significant low probability, 4.5%, of this occurring by chance. The apparent differences in degradation rates between control and ivermectin treated pats exposed in August were not significant.

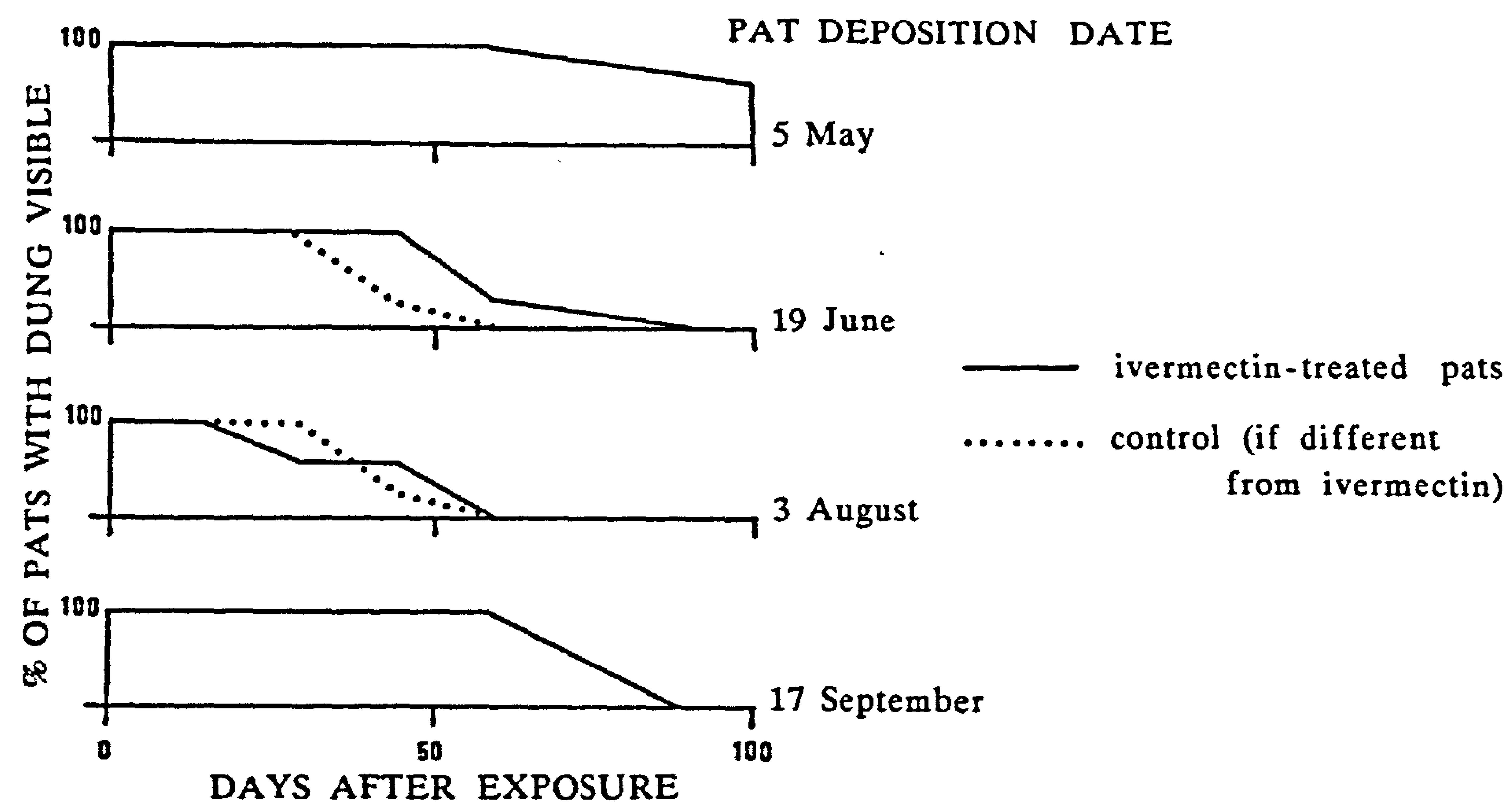


Fig. 8.12. Percentages of pats in each of the plots with dung visible after exposure on pasture. After 15, 30, 45, 60 and 90 days of exposure, 12 pats (9 treated and 3 controls) should have been sampled from each plot. The percentage figures in the diagram are related to the numbers of these ivermectin-treated and control pats with dung visible on each day of sampling.

DISCUSSION

Jackson (1989) reported that the manufacturer's estimate of the maximum concentration of ivermectin in faeces produced by cattle treated with the recommended, single, 200 mcg/kg body weight subcutaneous dose was 353 mcg/kg dung (or approximately 0.4 mg/kg). The levels used in this experiment were therefore very close to the levels expected under normal field conditions. In addition, although the dung used was not fresh (in that it had been kept in cold storage), insects colonised it and therefore any faunal differences between pats cannot be attributed to differences in the attractiveness of the dung.

The results clearly show that the presence of ivermectin markedly changed the fauna in, and below, the dung of treated pats. Ivermectin particularly affected Cyclorrhaphan fly larvae (Sepsidae, Scathophagidae, Muscidae and Sphaeroceridae), appearing to inhibit larval development and/or prevent pupation from taking place. In addition, such a change in fauna significantly reduced the decomposition rate of treated pats placed on pasture at the beginning of summer.

This corresponds well with the results of a previous investigation (Schmidt, 1983), where the emergence of Sepsidae, Sphaeroceridae and two species of *Gymnodia* (Muscidae) was found to be severely reduced in the manure from animals treated with a single standard dose of ivermectin. Recent research in Denmark (Madsen *et al.*, 1990), using dung from cattle treated with a standard dose of ivermectin, also showed a similar effect on Cyclorrhaphan larvae and pupae, as well as on Nematoceran larvae and pupae and *Aphodius* spp. larvae.

Madsen *et al.* (1990) also found that the decomposition of fresh faeces, collected from cattle 1 and 20 days after treatment with ivermectin, was delayed significantly when compared with untreated controls. As no adverse effects of treatment were recorded on earthworms, the retarded decomposition rate was ascribed to the adverse effects on the primary dipteran decomposing fauna.

McKeand *et al.* (1988) and Jacobs *et al.* (1988) studied the degradation of cow dung containing ivermectin in west-central Scotland and south-east England, respectively, and found no significant effect of ivermectin on dung breakdown. However, both trials were carried out during periods of wet weather, which may have contributed significantly to pat degradation, and neither group of researchers studied the invertebrate fauna of the dung.

As in Eyre *et al.* (1989) and Eyre *et al.* (1990a), analysis of the data by the direct CANOCO method did not provide a better understanding of the processes affecting community distribution than that achieved using the indirect methods associated with DECORANA. This would confirm the suggestion by Eyre *et al.* (1990a) that CANOCO has no obvious advantage over indirect methods in the analysis of the factors affecting the distribution of communities in complex systems.

CHAPTER NINE:
HPLC ANALYSIS OF IVERMECTIN
IN COW DUNG

INTRODUCTION

A number of papers have been published concerning high-performance liquid chromatography (HPLC) determination of ivermectin in plasma (Tolan *et al.*, 1980; Pivnichny *et al.*, 1983; Schnitzerling & Nolan, 1985; Kojima *et al.*, 1987; Oehler & Miller, 1989), animal tissue (Tway *et al.*, 1981; Chiu *et al.*, 1985; Slanina *et al.*, 1989) and milk (Alvinerie *et al.*, 1987; Toutain *et al.*, 1988), but, although Nessel *et al.* (1989) provide a summary of their procedure, no method has yet been described in detail for the determination of ivermectin in faeces.

From the results reported in the previous chapter it can be seen that a method for assessing the ivermectin concentration in faeces is required, and therefore an attempt to analyse ivermectin in cow dung is described here.

MATERIALS AND METHODS

Chemicals

All chemicals used were analytical grade purity. The commercially available product 'Ivomec' (containing 1% w/v ivermectin) was used to prepare the samples and standard solutions. Samples containing known amounts (2.0, 1.0, 0.6, 0.2 and 0 mg/kg) of ivermectin were prepared by spiking fresh cow dung as described in Chapter 8. Standard solutions (2-20 mcg/ml ivermectin in mobile phase) were used to run a standard curve.

Apparatus

A Gilson constant flow high-performance liquid chromatograph consisting of model 303 pumps and a model HM holochrome detector was used. The column (250 x 4.6 mm ID) contained 5 mcm Spherisorb ODS2; the mobile phase was methanol/tetrahydrofuran/water 65:19:16; the system was operated at ambient temperature at a flow rate of 1.4 ml/min; and the wavelength of the detector was set at 246 nm.

Procedure

10 g of sample was added to 50 ml of methanol, shaken for 1 hour, and filtered under vacuum through a layer of celite filter-aid. The resulting extract was concentrated on a rotary evaporator and redissolved in 20 ml of acetone. To precipitate pigments, 20 ml coagulation solution (10 g ammonium chloride and 20 ml orthophosphoric acid in 800 ml water) and 2.5 g celite were added, and the solution swirled occasionally for 45 mins. It was then filtered under vacuum and the extract added to 125 ml of 2% w/v sodium sulphate solution in a seperating funnel. Ivermectin was extracted with two 15 ml portions of trimethylpentane, and the combined organic layers were passed through anhydrous sodium sulphate into a 50 ml volumetric flask. The sodium sulphate was washed with trimethylpentane and the extract made up to volume.

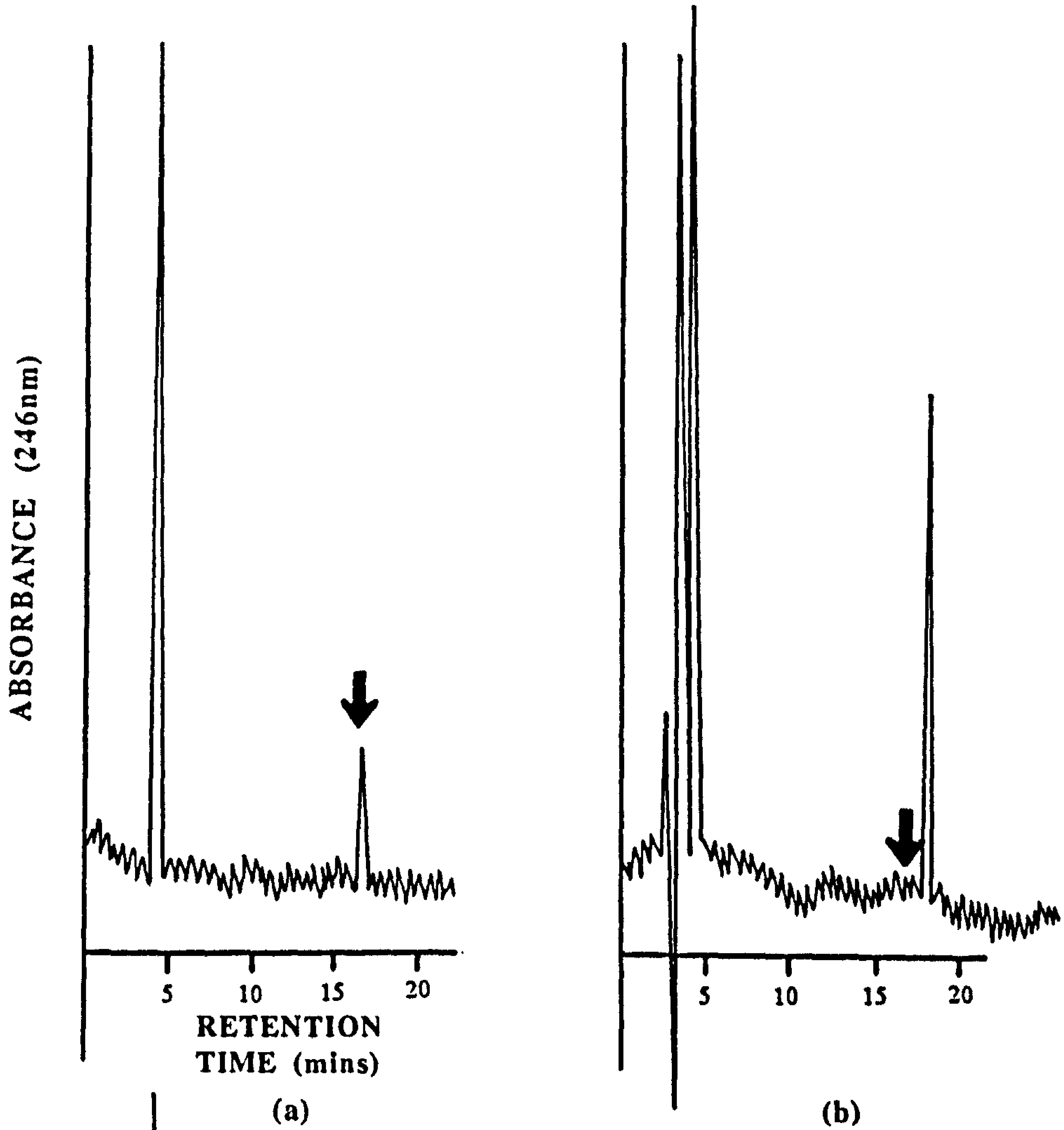
A 25 ml aliquot of the extract was evaporated to dryness, and the residue redissolved in 2 ml cyclohexane/dichloromethane 1:1 and applied to 1 g of carbon/celite 1:9 in a bond-elute cartridge. 10 ml cyclohexane/dichloromethane 1:1 was used to rinse the flask and added to the cartridge, which was then eluted further by adding 20 ml acetonitrile/toluene 3:1. All eluate was collected and evaporated to dryness, then redissolved in 0.25 ml chloroform and 1.25 ml hexane before being applied to an aminopropyl bond-elute cartridge. The cartridge was eluted with 10 ml hexane/isopropanol 96:4 and the eluate discarded. Ivermectin was eluted with 30 ml hexane/isopropanol 70:30, the extract was evaporated to dryness and redissolved in 1 ml mobile phase. 20 mcl of samples and standards were injected for HPLC analysis.

RESULTS

When the standard curve was run at 0.05 AUFS (Absorption Units Full Scale) a very small peak was obtained for the 20 mcg/ml standards 15.5 mins after injection, and so the sensitivity of the detector was increased to 0.02 AUFS. At this sensitivity the baseline was very 'noisy' and peaks were only detectable for the 20 and 10 mcg/ml standards. The peak heights for the three replicates at each of these two concentrations gave a regression line of $y = 1.66 + 0.7x$ (x=concentration; y=peak height) with a highly significant correlation coefficient of 0.978 ($P < 0.001$ with 4 d.f.).

After the extraction process described above, the concentration of the spiked dung samples should have been in the range 1-10 mcg/ml, and therefore only those samples containing the highest concentration would have been expected to produce detectable peaks. No such peaks were detected.

Representative chromatograms are shown in Fig. 9.1. In the chromatogram obtained from a blank dung sample (Fig. 9.1b) no peak is present which might interfere with the determination of ivermectin. Fig 9.1c shows the chromatogram of dung spiked with 2.0 mg/kg ivermectin (i.e. 10 mcg/ml in final analysis) with no detectable ivermectin peak.



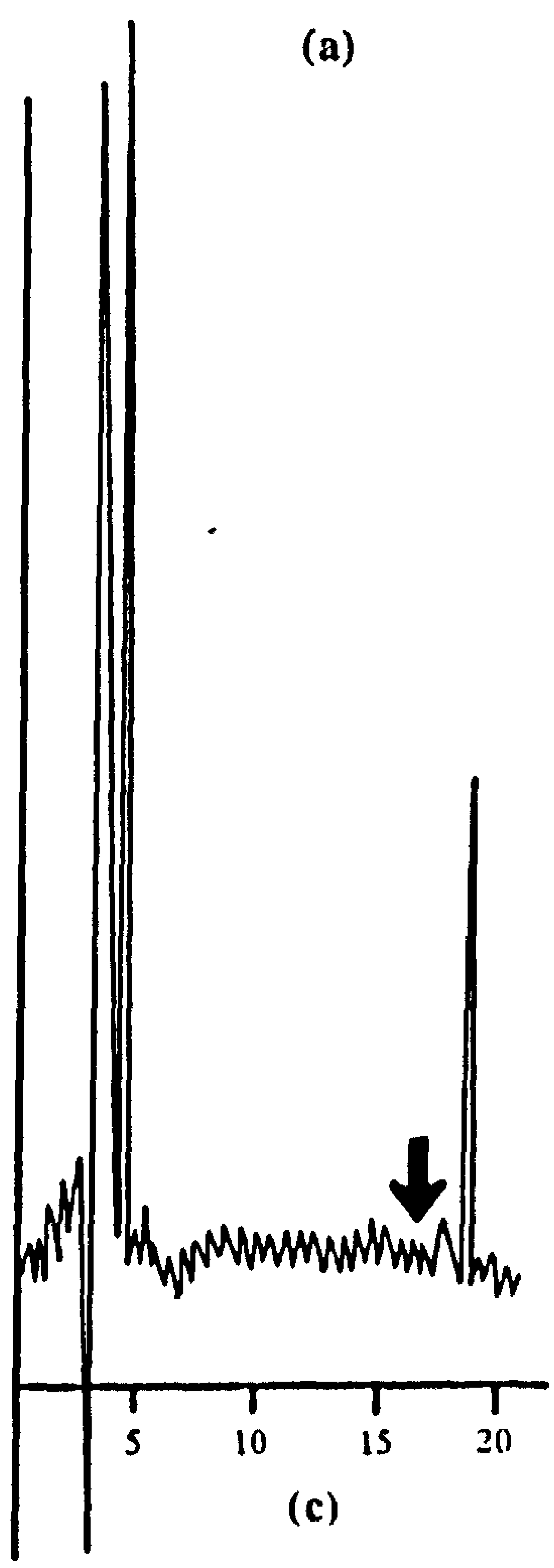


Fig. 9.1.
(a) chromatogram of a standard, 20 mcg/ml ivermectin;
(b) chromatogram obtained from a blank dung sample;
(c) chromatogram obtained from an extract of dung spiked with 2.0 mg ivermectin /kg dung.
The arrow indicates the ivermectin peak in (a), and where the peak should have occurred in (b) and (c).

As it took over two days to run each set of five samples through the extraction and clean-up process described above, it was decided not to repeat the experiment, and instead to treat it as a learning exercise for any future attempts.

DISCUSSION

The failure of the above method to detect ivermectin in the spiked samples could be due to one of three reasons:
(1) the extraction process failed to extract the ivermectin from the samples;
(2) the extraction process did extract the ivermectin, but at levels below the sensitivity of the detector;
(3) during the 4 month period between extraction and analysis by HPLC, when they were stored in a refrigerator at 12°C, the ivermectin in the samples may have been degraded to undetectable levels.

It is impossible to pinpoint the exact reason for the failure at the moment. On reflection, although the amounts of ivermectin with which it was decided to spike the dung samples were probably closely related to the levels expected in the field (see previous chapter for explanation), it would have been better to spike the dung with much higher levels, and thereby provide conclusive evidence of whether or not the process was capable of extracting ivermectin.

CHAPTER TEN
GENERAL DISCUSSION

INTRODUCTION

Soil moisture content was the primary factor determining the composition of both the surface-active and soil-dwelling invertebrate faunas on Islay. Grazing intensity also had a major influence on the composition of the surface-active fauna. Both faunas were affected by seasonality, but the winter and summer differences were not as marked at the sand grassland sites as at the others.

The invertebrate fauna associated with cow pats on Islay was determined by seasonality and the age of the dung.

Potential invertebrate prey items were available to the chough at the sample sites throughout most of the year. However, between October/November and January there was a deficit of potential invertebrate prey items - few large surface-active invertebrates were present; Tipulidae larvae in the soil were too small to be useful prey items; and there was very little invertebrate activity in fresh cow dung.

Analysis of chough faeces showed that seasonality was important in determining chough diet on Islay. The birds exploited seasonal abundances of invertebrates, with the exception of Carabidae adults (which may be distasteful to them). Tipulidae and Bibionidae larvae in soil, and insects associated with cow dung were especially important. During the early winter (October - January) when invertebrate availability was low, cereal grains, probably obtained from cattle feeding stations or stubble fields, were extremely important in the diet. The location of the feeding sites on the island also influenced the type of prey taken.

In an experiment conducted at the College, the composition of the invertebrate fauna of cow dung was primarily determined by seasonality and age of the dung, as was found on Islay. In addition, however, the presence of ivermectin in these experimental cow pats had a marked effect on the dung fauna, especially those invertebrates shown to be important chough prey items on Islay.

With reference to the disturbance and stress concept put forward by Southwood (see Chapter 2), the above results would suggest, (1) that management, e.g. grazing intensity and use of ivermectin, was the main disturbance factor acting on the invertebrate communities associated with pasture; (2) that soil moisture content and ageing of cow dung were the main adversity factors; and (3) that seasonality was an important additional factor, which affected some communities, e.g. the dung and soil faunas, more than others, e.g. the surface-active fauna.

DISCUSSION

Monaghan *et al.* (1989) found that, on Islay, the distribution of chough breeding sites showed a fairly close association with the occurrence of the climatic zone $O_1H_3T_1$ - Hyperoceanic Humid Northern Temperate, which indicates, for Scotland, a comparatively warm and humid climate with a reduced annual temperature range due to oceanic influence (defined by Birse, 1971). They therefore presumed that the strong westerly bias in the chough's distribution was related to climatic influences on prey availability.

Tipulidae larvae are very important components of the chough's diet on Islay, and the species most commonly found at the sample sites was *Tipula paludosa* Meigen. The climate of Islay is very suitable for this species, as damp weather in late summer and autumn is required to ensure the survival of the large numbers of larvae hatching at this time (Coulson, 1962). However, Tipulidae larvae do not feature in the chough's diet until the spring of any year, by which time developing larvae have attained a size large enough for them to be suitable prey items. Therefore, although the climatic conditions of Islay are suitable for the development of these and other invertebrate prey items, there is an inevitable time-lag before they are of any benefit to the chough.

However, the climate of the island also allows out-wintering of large numbers of cattle. It is the presence of these cattle on pasture throughout the winter, especially during the early months of low invertebrate availability, that ensures the continuing survival of the chough on the island.

Several former chough breeding areas (such as Gigha, the Mull of Kintyre, Burrow Head in Wigtownshire, and the Ayrshire cliffs) are also of climatic type $O_1H_3T_1$, and therefore probably just as suitable for the development of invertebrate prey items as Islay. Monaghan *et al.* (1989) suggested that the increase in the proportion of arable farming at the expense of pastoral regimes in these areas may have contributed to the chough's decline, but it may also simply have been caused by farmers abandoning the practice of out-wintering cattle in these areas, and therefore depriving the chough of food (supplementary cattle feed) at such a critical time.

CONCLUSIONS

The main conclusions of this study are:

(1) Tipulidae larvae are extremely important components of the chough's diet. In most years, the relatively warm and wet weather of Islay probably allows large numbers of hatched larvae to survive in the soil, and subsequently ensures that large populations of maturing larvae are

available to the chough as prey items.

(2) The system of livestock farming on Islay, especially the practice of out-wintering cattle, is essential for providing good feeding opportunities for the chough, as (a) grazing produces the short sward preferred by chough as a feeding habitat; (b) large amounts of fresh dung are available throughout the year, with the result that dung-associated invertebrates can be active as far into the winter as the weather allows, and dung is available for colonisation immediately these invertebrates become active again in spring; and (c) grain provided as supplementary feed for the cattle during the winter is a very important alternative food source for the chough (as are the stubble fields in which it is grown).

(3) The chough's preference on Islay for feeding in sandy, coastal pasture, is probably due to the fact that these sites, (a) contain a variety of suitable soil-dwelling and surface-active invertebrate prey items throughout most of the year; (b) are normally intensively grazed and so also contain large amounts of dung with its associated fauna; and (c) are used for out-wintering cattle and therefore cereal grains can be found there.

(4) Treating cattle with ivermectin reduces the number and variety of invertebrates associated with their dung. This could have an adverse effect on the chough, especially if the cattle were treated during spring and autumn when cow dung is an important source of invertebrate food for the birds.

REFERENCES

ALVINERIE M., SUTRA J.F., GALTIER P. & TOUTAIN P.L. 1987. Determination of ivermectin in milk by high performance liquid chromatography. *Annales de Recherche Vétérinaire* **18** 269-274.

AMANO K. 1988. Ecological study of the dung-breeding flies, with special reference to the intra- and inter-specific larval competitions in cattle dung pats. Unpublished Ph.D. Thesis, Kyoto Prefectural University.

d'ASSIS FONESCA E.C.M. 1978. Diptera, Orthorrhapha, Brachycera: Dolichopodidae. *Handbooks for the Identification of British Insects* **9(5)** 1-90.

BIGNAL E.M., CURTIS D.J. & MATTHEWS J.L. 1988. *Islay: land types, bird habitats and nature conservation. Part 1: land use and birds on Islay.* NCC Chief Scientist Directorate Report **809, Part 1**. NCC Peterborough.

BIRSE E.L. 1971. *Assessment of climatic conditions in Scotland: the bioclimatic sub-regions*. Macaulay Land Use Research Institute, Aberdeen.

BOLTON B. & COLLINGWOOD C.A. 1975. Hymenoptera: Formicidae. *Handbooks for the Identification of British Insects* **11(3c)** 1-34.

BORNEMISSZA G.F. 1976. The Australian dung beetle project 1965-1975. *Australian Meat Research Committee Review* **30** 1-30.

BRAUNS A. 1954a. *Terricole Dipterenlarven*. Musterschmidt, Göttingen.

BRAUNS A. 1954b. *Puppen terricoler Dipterenlarven*. Musterschmidt, Göttingen.

BRINDLE A. 1960. The larvae and pupae of the British Tipulinae (Diptera: Tipulidae). *Transactions of the Society for British Entomology* 14 63-114.

BRINDLE A. 1962a. Taxonomic notes on the larvae of British Diptera. 6. The family Bibionidae. *The Entomologist* 95 22-26.

BRINDLE A. 1962b. Taxonomic notes on the larvae of British Diptera. 11. Trichoceridae and Anisopodidae. *The Entomologist* 95 284-288.

BRINDLE A. 1977. British Earwigs (Dermaptera). *Entomologist's Gazette* 28 29-37.

BRINDLE A. & SMITH K.G.V. 1978. The immature stages of flies. In: A *Dipterist's Handbook* eds. A. Stubbs & P. Chandler. 38-64. The Amateur Entomologists' Society. Hanworth, Middlesex.

BULLOCK I.D. 1980. Some aspects of the ecology of the chough *Pyrrhocorax pyrrhocorax* at South Stack, Anglesey, November 1978 - October 1979. Unpublished M.Sc. Thesis, University of Wales.

BULLOCK I.D., DREWETT D.R. & MICKLEBURGH S.P. 1983. The chough in Britain and Ireland. *British Birds* 76 377-401.

BURG R.W., MILLER B.M., BAKER E.E., BIRNBAUM J., CURRIE S.A., HARTMAN R., KONG Y.L., MONAGHAN R.L., OLSON G., PUTTER I., TANAC J.B., WALLICK H., STAPLEY E.O., OIWA R. & OMURA S. 1979. Avermectins, new family of potent anthelmintic agents: producing organism and fermentation. *Antimicrobial Agents Chemotherapy* 15 361-367.

CAMPBELL W.C. 1985. Ivermectin: an update. *Parasitology Today* 1 10-16.

CAMPBELL W.C. 1989 (ed.). *Ivermectin and Abamectin*. Springer, New York.

CARLETON T.J. 1985. *ECOSURVEY: programmes for the analysis of ecological survey data on the IBM/PC microcomputer.* University of Toronto, Toronto.

CHVALA M., LYNEBORG L. & MOUCHA J. 1972. *The Horse Flies of Europe (Diptera: Tabanidae).* The Entomological Society of Copenhagen, Copenhagen.

CHIU S.H.L., BUHS R.P., SESTOKAS E., TAUB R. & JACOB T.A. 1985. Determination of ivermectin residue in animal tissues by high-performance liquid chromatography-reverse isotope dilution assay. *Journal of Agricultural and Food Chemistry* **33** 99-102.

COULSON J.C. 1962. The biology of *Tipula subnodicornis* Zetterstedt, with comparative observations on *Tipula paludosa* Meigen. *Journal of Animal Ecology* **31** 1-21.

COULSON J.C. & BUTTERFIELD J.E.L. 1985. The invertebrate communities of peat and upland grasslands in the north of England and some conservation implications. *Biological Conservation* **35** 197-225.

COWDY S. 1973. Ants as a major food source of the chough. *Bird Study* **20** 117-120.

CURRY J.P. 1987a. The invertebrate fauna of grassland and its influence on productivity. 1. The composition of the fauna. *Grass and Forage Science* **42** 103-120.

CURRY J.P. 1987b. The invertebrate fauna of grassland and its influence on productivity. 2. Factors affecting the abundance and composition of the fauna. *Grass and Forage Science* **42** 197-212.

CURRY J.P. 1987c. The invertebrate fauna of grassland and its influence on productivity. 3. Effects on soil fertility and plant growth. *Grass and Forage Science* **42** 325-341.

CURRY J.P. & COTTON D.C.F. 1983. Earthworms and land reclamation. In: *Earthworm Biology* ed. J.E. Satchell, Chapman and Hall, London.

CURTIS D.J., CURTIS E.J., BIGNAL E. & CORRIGAN H. 1988. Land-type selection and vegetation-type selection by choughs on Islay. In: *Choughs and Land-use in Europe* eds. E. Bignal & D.J. Curtis. 94-101. Scottish Chough Study Group. Clachan, Tarbert, Argyll.

DENHOLM-YOUNG P. 1978. Studies of decomposing cattle dung and its associated fauna. Unpublished Ph.D. Thesis, University of Oxford.

DESIERE M. 1973. Ecologie des coléoptères coprophages. *Annales de la Societé Royal Zoologique de Belgique* **103** 135-145.

DETTNER K. 1987. Chemosystematics and evolution of beetle chemical defenses. *Annual Review of Entomology* **32** 17-48.

DOUBE B.M. 1987. Spatial and temporal organization in communities associated with dung pads and carcasses. In: *Organization of Communities - Past and Present*. 255-280. eds. J.H.R. Gee and P.S. Giller. Blackwell Scientific, Oxford.

DOUBE B.M., MacQUEEN A. & FAY H.A.C. 1988. Effects of dung fauna on survival and size of buffalo flies (*Haematobia* spp.) breeding in the field in South Africa and Australia. *Journal of Applied Ecology* **25** 523-536.

EGERTON J.R., BIRNBAUM J., BLAIR L.S., CHABALA J.C., CONROY J., FISHER M.H., MROZIK H., OSTLIND D.A., WILKINS C.A. & CAMPBELL W.C. 1979. Avermectins, new family of potent anthelmintic agents: efficacy of the B_{1a} component. *Antimicrobial Agents Chemotherapy* **15** 372-378.

van EMDEN F.I. 1942. Larvae of British Beetles. 3. Keys to the families. *Entomologist's Monthly Magazine* **78** 206-272.

van EMDEN F.I. 1945. Larvae of British Beetles. 5. Elateridae. *Entomologist's Monthly Magazine* **81** 13-37.

EYRE M.D., BALL S.G. & FOSTER G.N. 1986. An initial classification of the habitats of aquatic Coleoptera in north-east England. *Journal of Applied Ecology* **23** 841-852.

EYRE M.D., LUFF M.L., RUSHTON S.P. & TOPPING C.J. 1989. Ground beetles and weevils (Carabidae and Curculionoidea) as indicators of grassland management practices. *Journal of Applied Entomology* **107** 508-517.

EYRE M.D., FOSTER G.N. & FOSTER A.P. 1990a. Factors affecting the distribution of water beetle species assemblages in drains of eastern England. *Journal of Applied Entomology* **109** 217-225.

EYRE M.D., LUFF M.L. & RUSHTON S.P. 1990b. The ground beetle (Coleoptera: Carabidae) fauna of intensively managed agricultural grasslands in northern England and southern Scotland. *Pedobiologia* (in press).

FOSTER G.N., McCRACKEN D.I., LUFF M.L., RUSHTON S.P. & EYRE M.D. 1990. Pesticide studies on non-target invertebrates in a wider environmental context. *Proceedings Crop Protection in Northern Britain 1990* 153-158.

FREEMAN P. 1983. Sciarid Flies. Diptera: Sciaridae. *Handbooks for the Identification of British Insects* **9(6)** 1-68.

FREEMAN P. & LANE R.P. 1985. Bibionid and Scatopsid Flies. Diptera: Bibionidae and Scatopsidae. *Handbooks for the Identification of British Insects* **9(7)** 1-74.

GATEHOUSE A.G. & MORGAN M.J. 1973. Notes on the predation of Coleoptera in sheep dung by choughs in north Wales. *Nature in Wales* **13** 267.

GAUCH H.G. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.

GIBBONS D.S. 1987. The causes of seasonal changes in numbers of the yellow dung fly, *Scathophaga stercoraria* (Diptera: Scathophagidae). Ecol. Ent. 12 173-185.

GREEN F.H.W. & HARDING R.J. 1983. Climate of the Inner Hebrides. *Proceedings of the Royal Society of Edinburgh* **83B** 121-140.

GREENSLADE P.J.M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *Journal of Animal Ecology* **33** 301-310.

HAMMER O. 1941. Biological and ecological investigations on flies associated with pasturing cattle and their excrement. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening* **105** 141-393.

HANSEN M. 1987. The Hydrophiloidea (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* **18**.

HANSKI I. 1980a. Spatial patterns and movements in coprophagous beetles. *Oikos* **34** 293-310.

HANSKI I. 1980b. Spatial variation in the timing of the seasonal occurrence in coprophagous beetles. *Oikos* **34** 311-321.

HANSKI I. 1980c. Patterns of beetle succession in droppings. *Annales Zoologici Fennici* **17** 17-25.

HANSKI I. 1980d. The community of coprophagous beetles (Coleoptera, Scarabaeidae and Hydrophilidae) in northern Europe. *Annales Entomologici Fennici* **46** 57-73.

HANSKI I. 1986. Individual behaviour, population dynamics and community structure of *Aphodius* (Scarabaeidae) in Europe. *Acta Oecologica/Oecologica Generalis* **7** 171-182.

HANSKI I. & KOSKELA H. 1977. Niche relations among dung-inhabiting beetles. *Oecologia (Berlin)* **28** 203-231.

HENNIG W. 1948-52. *Die Larvenformen der Diptera*. 3 Vols. Akademie, Berlin.

HILL M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. *Journal of Ecology* 61 237-249.

HILL M.O. 1979a. *TWINSPAN - a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes*. Cornell University, Ithaca, New York.

HILL M.O. 1979b. *DECORANA - a FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Cornell University, Ithaca, New York.

HOLTER P. 1974. Food utilization of dung-eating *Aphodius* larvae (Scarabaeidae). *Oikos* 25 71-79.

HOLTER P. 1977. An experiment in dung removal by *Aphodius* larvae (Scarabaeidae) and earthworms. *Oikos* 28 130-136.

HOLTER P. 1979. Effect of dung beetles (*Aphodius* spp.) and earthworms on the disappearance of cattle dung. *Oikos* 32 393-402.

HOLYOAK D. 1967. Food and feeding actions of Choughs. *Bird Study* 14 61-62.

JACKSON H.C. 1989. Ivermectin as a systemic insecticide. *Parasitology Today* 5 146-156.

JACOBS D.E., PILKINGTON J.G., FISHER M.A. & FOX M.T. 1988. Ivermectin therapy and degradation of cattle faeces. *Veterinary Record* 123 400.

JESSOP L. 1986. Dung Beetles and Chafers. Coleoptera: Scarabaeoidea. *Handbooks for the Identification of British Insects* 5(11) 1-53.

JOY N.H. 1932. A *Practical Handbook of British Beetles*. 2 Vols. Witherby, London.

KLOET G.S. & HINCKS W.D. 1964. A check list of British insects. Part 1: Small orders and Hemiptera. *Handbooks for the Identification of British Insects* **11(1)** 1-119.

KLOET G.S. & HINCKS W.D. 1976. A check list of British insects. Part 5: Diptera and Siphonaptera. *Handbooks for the Identification of British Insects* **11(5)** 1-139.

KLOET G.S. & HINCKS W.D. 1977. A check list of British insects. Part 3: Coleoptera and Strepsiptera. *Handbooks for the Identification of British Insects* **11(3)** 1-105.

KLOET G.S. & HINCKS W.D. 1978. A check list of British insects. Part 4: Hymenoptera. *Handbooks for the Identification of British Insects* **11(4)** 1-159.

KOJIMA K., YAMAMOTO K., NAKANISHI Y. & KATAE H. 1987. Determination of 22,23-dihydroavermectin B_{1a} in dog plasma using solid-phase extraction and high-performance liquid chromatography. *Journal of Chromatography* **413** 326-331.

KOSKELA H. & HANSKI I. 1977. Structure and succession in a beetle community inhabiting cow dung. *Annales Zoologici Fennici* **14** 204-223.

KRIVOSEINA N.P. 1962. Die Europäischen Bibionidae-Larven. *Pedobiologia* **1** 210-227.

KUMAR R. & LLOYD J.E. 1976. A bibliography of the arthropods associated with dung. *Science Series Colorado State University Range Science Department* **18** 1-33.

LANDIN B.O. 1961. Ecological studies on dung beetles. *Opuscula Entomologica (Supplementum)* **19** 1-228.

LAURENCE B.R. 1954. The larval inhabitants of cow pats. *Journal of Animal Ecology* **23** 234-260.

LINDROTH C.H. 1974. Coleoptera: Carabidae. *Handbooks for the Identification of British Insects* **4(2)** 1-148.

LUFF M.L. 1975. Some features influencing the efficiency of pitfall traps. *Oecologia* **19** 345-357.

LUFF M.L. 1987. Biology of polyphagous ground beetles in agriculture. *Agricultural Zoology Reviews* **2** 237-278.

LUFF M.L. & EYRE M.D. 1988. Soil-surface activity of weevils (Coleoptera: Curculionoidea) in grassland. *Pedobiologia* **32** 39-46.

LUFF M.L. & RUSHTON S.P. 1989. The ground beetle and spider fauna of managed and unimproved upland pasture. *Agriculture, Ecosystems and Environment* **25** 195-205.

LUFF M.L., EYRE M.D. & RUSHTON S.P. 1989. Classification and ordination of habitats of ground beetles (Coleoptera: Carabidae) in north-east England. *Journal of Biogeography* **16** 121-130.

McCRACKEN D.I. 1987. The use of ivermectin and implications for wildlife. Unpublished Report to the NCC, Peterborough.

McKEAND J., BAIRDEN K. & IBARRA-SILVA A.M. 1988. The degradation of bovine faecal pats containing ivermectin. *Veterinary Record* **122** 587-588.

MADSEN M., NIELSEN B.O., HOLTER P., PEDERSEN O.C., JESPERSEN J.B., VAGN JENSEN K.M., NANSEN P. & GRONVOLD J. 1990. Treating cattle with ivermectin: effects on the fauna and decomposition of dung pats. *Journal of Applied Ecology* **27** 1-15.

MERRITT R.W. & ANDERSON J.R. 1977. The effects of different pasture and rangeland ecosystems on the annual dynamics of insects in cattle droppings. *Hilgardia* **45** 31-71.

METEOROLOGICAL OFFICE 1988. *Monthly Weather Report* **105**

METEOROLOGICAL OFFICE 1989. *Monthly Weather Report* **106**

MEYER J.A., SIMCO J.S. & LANCASTER J.L. 1981. Control of face fly larval development in bovine faeces with daily injections of the ivermectin, MK-933. *Southwestern Entomologist* 6 269-271.

MILLER J.A., KUNZ S.E., OEHLER D.D. & MILLER R.W. 1981. Larvicidal activity of Merck MK-933, an avermectin, against the horn fly, stable fly, face fly and house fly. *Journal of Economic Entomology* **74** 608-611.

MILLER T.W., CHAIET L., COLE D.J., COLE L.J., FLOR J.E., GOEGELMAN R.T., GULLO V.P., JOSHUA H., KEMPF A.J., KRELLWITZ W.R., MONAGHAN R.L., ORMOND R.E., WILSON K.E., ALBERS-SCHONBERG G. & PUTTER I. 1979. Avermectins, new family of potent anthelmintic agents: isolation and chromatographic properties. *Antimicrobial Agents Chemotherapy* **15** 368-371.

MOHR C.O. 1943. Cattle droppings as ecological units. *Ecological Monographs* **13** 275-309.

MONAGHAN P. 1988a. The background to chough studies in Britain. In: *Choughs and Land-use in Europe* eds. E. Bignal & D.J. Curtis. 4-8. Scottish Chough Study Group. Clachan, Tarbert, Argyll.

MONAGHAN P. 1988b. Communal roosting and social behaviour of choughs. In: *Choughs and Land-use in Europe* eds. E. Bignal & D.J. Curtis. 63-64. Scottish Chough Study Group. Clachan, Tarbert, Argyll.

MONAGHAN P., BIGNAL E., BIGNAL S., EASTERBEE N. & McKAY C.R. 1989. The distribution and status of the chough in Scotland in 1986. *Scottish Birds* **15** 114-118.

MORRIS M.G. & RISPIN W.E. 1987. Abundance and diversity of the coleopterous fauna of a calcareous grassland under different cutting regimes. *Journal of Applied Ecology* **24** 451-465.

NESSEL R.J., WALLACE D.H., WEHNER T.A., TAIT W.E. & GOMEZ L. 1989. Environmental fate of ivermectin in a cattle feedlot. *Chemosphere* **18** 1531-1541.

NORDSTROM S. & RUNDGREN S. 1974. Environmental factors and lumbricid associations in southern Sweden. *Pedobiologia* **14** 1-27.

OEHLER D.D. & MILLER J.A. 1989. Liquid chromatographic determination of ivermectin in bovine serum. *Journal of the Association of Official Analytical Chemists* **72** 59.
PALM T. 1972. *Die Skandinavischen Elateriden-Larven (Coleoptera)*. Munksgaard, Copenhagen.

PARKER G.A. 1970. The reproductive behaviour and the nature of sexual selection in *Scathophaga stercoraria* (L.) (Diptera: Scathophagidae). I. Diurnal and seasonal changes in population density around the site of mating and oviposition. *Journal of Animal Ecology* **39** 185-204.

PERSSON T. & LOHM U. 1977. *Energetical significance of the annelids and arthropods in a Swedish grassland soil*. Swedish Natural Science Research Council, Stockholm.

PETERSON A. 1977. *Larvae of Insects*. 2 Vols. Edwards Brothers, Michigan.

PITKIN B.R. 1988. Lesser dung flies. Diptera: Sphaeroceridae. *Handbooks for the Identification of British Insects* **10(5e)** 1-175.

PIVNICHNY J.V., SHIM J.S.K. & ZIMMERMAN L.A. 1983. Direct determination of avermectins in plasma at nanogram levels by high-performance liquid chromatography. *Journal of Pharmaceutical Sciences* **72** 1447-1450.

PUTMAN R.J. 1983. Carrion and dung: the decomposition of animal wastes. *Studies in Biology* **156** 1-62.

RIDSDILL-SMITH T.J. 1988a. Some effects of avermectins on non-target organisms in cattle dung. *Proceedings of the 5th Australian Conference on Grassland Invertebrate Ecology - Melbourne, 1988* (in press).

RIDSDILL-SMITH T.J. 1988b. Survival and reproduction of *Musca vetustissima* Walker (Diptera: Muscidae) and a scarabaeine dung beetle in dung of cattle treated with avermectin B_1. *Journal of the Australian Entomological Society* **27** 175-178.

ROBERTS P.J. 1982. Foods of the chough on Bardsey Island, Wales. *Bird Study* **29** 155-161.

ROLFE R. 1966. The status of the chough in the British Isles. *Bird Study* **13** 221-226.

ROOT R.B. 1967. The niche exploitation pattern of the blue-grey gnat catcher. *Ecological Monographs* **37** 317-350.

RUSHTON S.P., LUFF M.L. & EYRE M.D. 1989. Effects of pasture improvement and management on the ground beetle and spider communities of upland grasslands. *Journal of Applied Ecology* **26** 489-503.

SCHMIDT C.D. 1983. Activity of an avermectin against selected insects in aging manure. *Environmental Entomology* **12** 455-457.

SCHMIDT C.D. & KUNZ S.E. 1980. Testing immature, laboratory-reared stable flies (*Stomxys calcitrans*) and horn flies (*Haematobia irritans*) for susceptibility to insecticides. *Journal of Economic Entomology* **704** 608-611.

SCHNITZERLING H.J. & NOLAN J. 1985. Normal phase liquid chromatographic determination of nanogram quantities of ivermectin in cattle blood or plasma. *Journal of the Association of Official Analytical Chemists* **68** 36-40.

SLANINA P., KUIVINEN J., OHLSEN C. & EKSTROM L.G. 1989. Ivermectin residues in the edible tissues of swine and cattle: effect of cooking and toxicological evaluation. *Food Additives and Contaminants* **6** 475-481.

SKIDMORE P. 1985. *The biology of the Muscidae of the world.* Dr W. Junk, Dordrecht.

SKIDMORE P. 1989. *The Insects of the Cow Dung Community.* Field Studies Council, Taunton.

SMIDDY P. 1986. Choughs feeding on top of vegetation. *British Birds* **79** 251-252.

SMITH K.G.V. 1989. An introduction to the immature stages of British flies. *Handbooks for the Identification of British Insects* **10(14)** 1-280.

SOUTHWOOD T.R.E. 1978. *Ecological Methods.* Chapman and Hall, London.

SOUTHWOOD T.R.E. 1987. The concept and nature of the community. In: *Organization of Communities - Past and Present* 3-27 eds. J.H.R. Gee and P.S. Giller. Blackwell Scientific, Oxford.

SUNDERLAND K.D. 1975. The diet of some predatory arthropods in cereal crops. *Journal of Applied Ecology* **12** 507-515.

SUNDERLAND K.D. & VICKERMAN G.P. 1980. Aphid feeding by some polyphagous predators in relation to aphid density in cereal fields. *Journal of Applied Ecology* **17** 389-396.

TER BRAAK C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* **67** 1167-1179.

TER BRAAK C.J.F. 1987. *CANOCO - a FORTRAN program for canonical community ordination by partial detrended correspondence analysis, principal components analysis and redundancy analysis (version 2.1)*. TNO Institute of Applied Computer Science, Wageningen.

THEOWALD B. 1967. *Familie Tipulidae (Diptera: Nematocera). Larven und Puppen*. Akademie, Berlin.

THIELE H.-U. 1977. *Carabid beetles in their environments*. Springer, Berlin.

TOLAN J.W., ESKOLA P., FINK D.W., MROZIK H. & ZIMMERMAN L.A. 1980. Determination of avermectins in plasma at nanogram levels using high-performance liquid chromatography with fluorescence detection. *Journal of Chromatography* **190** 367-376.

TOTTENHAM C.E. 1954. Coleoptera: Staphylinidae. Section (a) Piestinae to Euaesthetinae. *Handbooks for the Identification of British Insects* **4(8a)** 1-79.

TOUTAIN P.L., CAMPAN M., GALTIER P. & ALVINERIE M. 1988. Kinetic and insecticidal properties of ivermectin residues in the milk of dairy cows. *Journal of Veterinary Pharmacology and Therapeutics* **11** 288-291.

TWAY P.C., WOOD J.S. & DOWNING G.V. 1981. Determination of ivermectin in cattle and sheep tissues using high-performance liquid chromatography with fluorescence detection. *Journal of Agricultural and Food Chemistry* **29** 1059-1063.

UNWIN D.M. 1984. A key to the families of British Coleoptera (and Strepsiptera). *Field Studies* **6** 149-197.

VALIELA I. 1974. Composition, food webs and population limitation in dung arthropod communities during invasion and succession. *American Midland Naturalist* **92** 370-385.

WALL R. & STRONG L. 1987. Environmental consequences of treating cattle with the antiparasitic drug ivermectin. *Nature* **327** 418-421.

WARD P.I. & SIMMONS L.W. 1990. Short-term changes in the numbers of the yellow dung fly *Scathophaga stercoraria* (Diptera: Scathophagidae). Ecol. Ent. 15 115-118

WARDHAUGH K.G. & RODRIGUEZ-MENENDEZ H. 1988. The effects of the antiparasitic drug, ivermectin, on the development and survival of the dung-breeding fly, *Orthelia cornicina* (F.) and the scarabaeine dung beetles, *Copris hispanus* L., *Bubas bubalus* (Oliver) and *Onitis belial* F.. *Journal of Applied Entomology* **106** 381-389.

WARNES J.M. 1982. A study of the ecology of the chough *Pyrrhocorax pyrrhocorax* L. on the Isle of Islay, Argyll, 1980 - 1981. Unpublished M.Sc. Thesis, University of Stirling.

WARNES J.M. 1983. The status of the chough in Scotland. *Scottish Birds* **12** 238-246.

WATERHOUSE D.F. 1974. The biological control of dung. *Scientific American* **230** 100-109.

WRIGHT J.F., MOSS D., ARMITAGE P.D. & FURSE M.T. 1984. A preliminary classification of running-water sites in Great Britain based on macro-invertebrate species and the prediction of community type using environmental data. *Freshwater Biology* **14** 221-256.

APPENDIX 1. Taxa abundances in pitfall traps on Islay. Taxa numbers (as in Table 4.2) with corresponding abundance values are shown for each subsample (Table 4.1).

AA01	5	6	8	3	12	3	14	3	19	3	59	9								
AA02	2	40	4	6	13	12	14	6	30	3	34	6	41	3	53	9	59	90	62	3
AA03	2	51	4	3	9	3	13	63	14	15	22	3	25	3	26	3	30	3	31	3
AA03	36	12	41	18	47	24	52	3	53	48	57	3	59	15						
AA04	2	27	4	18	13	66	14	117	25	21	26	48	41	3	53	135	56	6	59	15
AA05	4	18	9	9	13	86	14	76	30	72	33	4	36	4	53	660	56	9	59	4
AA06	2	54	8	9	9	27	19	36	30	54	38	9	53	54	56	126	59	18		
AA07	9	14	36	4	53	68	56	4	59	4										
AA08	9	27	19	12	40	3	53	201	56	3										
AA09	2	76	4	9	9	9	12	9	13	9	14	4	19	9	30	4	36	9	53	166
AA09	56	4	59	86																
AB01	5	1	7	3	10	1	11	1	12	1	13	1	14	3	19	21	30	700	32	1
AB01	33	1	34	20	36	34	37	31	39	3	40	2	41	26	45	4	47	8	52	5
AB01	53	244	56	34	57	11	59	190	62	4										
AB02	2	39	4	1	5	10	7	2	8	1	12	4	13	1	14	1	19	8	30	870
AB02	32	1	33	1	34	26	36	33	37	24	39	4	40	16	41	16	45	3	47	6
AB02	48	1	52	2	53	92	56	29	57	20	59	139								
AB03	2	5	4	1	9	2	11	2	13	7	14	21	19	17	30	397	31	3	33	1
AB03	34	6	36	1	37	4	40	15	41	2	45	2	47	4	51	1	52	2	53	410
AB03	56	27	59	67	61	86	62	2												
AB04	2	5	4	2	5	1	7	1	13	6	14	24	19	19	22	6	30	295	33	2
AB04	36	1	37	7	40	13	41	2	47	3	51	2	52	1	53	251	56	21	57	3
AB04	59	75	61	53																
AB05	4	4	6	19	9	2	11	3	13	2	14	14	19	11	22	4	37	1	40	2
AB05	47	1	53	300	56	5	59	24	61	66										
AB06	4	2	6	12	9	1	11	1	13	5	14	5	19	3	22	9	36	1	37	1
AB06	40	4	47	1	52	4	53	250	56	1	57	1	59	40	61	103	62	1		
AB07	4	1	6	14	12	1	13	4	19	28	28	2	32	1	36	7	37	2	40	1
AB07	47	16	52	9	53	45	56	18	59	10	61	72	62	6						
AB08	6	24	13	9	14	22	19	19	26	1	32	1	36	8	37	6	45	2	47	40
AB08	52	17	53	35	56	28	59	15	61	64	62	4								
BB01	2	15	12	3	19	81	27	20	32	3	38	48	53	138	54	18	56	24		
BB02	16	141	18	3	19	48	27	33	31	3	32	3	35	15	36	3	37	3	38	195
BB02	45	6	46	3	53	126	54	3	55	6										
BB03	13	3	14	6	16	75	17	6	27	540	29	3	35	9	36	42	38	126	45	6
BB03	53	312	55	21																
BB04	1	3	7	3	14	3	16	15	19	3	27	405	36	15	42	6	48	6	53	81
BB04	54	3	55	48																
BB05	14	9	15	12	17	3	20	9	27	640	30	90	33	21	35	33	36	81	38	69
BB05	42	21	43	21	45	6	48	9	49	6	53	183	55	15	56	3	60	3		
BB06	19	21	27	900	33	3	35	21	36	12	38	381	42	9	47	30	53	78	54	3
BB06	55	9	56	6	59	3														
BB07	2	9	19	69	27	852	35	3	38	111	47	60	53	201	54	48				
BB08	19	30	27	27	36	6	38	45	47	9	53	42	54	51	56	21	59	12		
BB09	16	72	19	15	27	78	35	3	36	3	38	60	53	78	54	15	55	3	59	3
BB10	13	2	16	20	19	5	20	1	26	1	27	51	32	1	33	1	35	10	36	23
BB10	37	7	38	20	39	2	42	1	44	1	45	2	48	1	49	2	53	245	54	4
BB10	55	22	56	3	62	2														
BB11	1	1	16	43	19	6	27	55	29	7	33	2	35	42	36	14	37	4	38	31
BB11	40	3	42	2	44	1	45	1	47	5	48	1	53	500	54	6	55	30	56	1

Appendix 1 cont:

BB11	57	1	59	5																
BB12	1	1	2	1	13	1	14	3	16	16	19	8	23	2	27	98	29	3	31	1
BB12	33	2	35	70	36	10	37	2	42	3	43	1	47	3	48	7	49	1	53	314
BB12	54	1	55	40	56	7	57	1	59	1										
BB13	1	1	4	1	13	1	14	1	16	10	19	6	23	3	27	93	29	3	31	1
BB13	35	65	36	14	39	1	42	1	43	7	47	3	48	3	49	3	53	395	55	50
BB13	56	4	57	1	59	2														
BB14	7	1	14	1	16	4	17	2	20	5	27	200	35	58	36	12	37	2	42	3
BB14	43	12	45	2	48	6	49	4	53	150	54	1	55	5	56	2				
BB15	13	1	14	6	16	2	20	5	27	270	31	1	36	7	37	3	43	8	45	4
BB15	48	3	49	1	53	124	54	3	55	3	58	1								
BB16	20	3	27	310	35	25	36	26	37	4	38	84	45	1	47	15	48	4	49	2
BB16	53	50	54	13	55	2	56	7												
BB17	14	2	19	1	20	2	27	420	35	20	36	49	38	50	39	2	42	1	43	1
BB17	46	1	47	20	48	2	53	40	54	9	56	3								
CA01	4	12	10	3	13	9	14	15	19	6	25	60	26	3	30	9	34	138	36	36
CA01	39	3	41	6	53	45	56	6	59	33	62	3								
CA02	2	18	4	9	13	147	14	429	25	3	26	147	27	6	33	9	34	24	45	9
CA02	53	15	59	12	61	27														
CA03	6	6	11	3	13	57	14	150	26	54	34	300	51	9						
CA04	2	6	13	9	14	9	19	39	28	3	33	24	34	39	36	30	47	3	53	12
CA04	56	51	61	36	62	6														
CA05	19	69	36	18	53	72	56	30	61	39	62	21								
CA06	19	21	34	15	36	3	53	183	54	3	56	30	61	18	62	12				
CA07	4	3	14	21	19	21	33	3	34	111	36	4	39	3	41	6	45	6	47	6
CA07	52	3	53	15	56	24	57	3	59	3										
CB01	2	9	4	14	5	3	11	2	12	7	13	5	14	3	19	137	21	11	24	164
CB01	28	10	33	1	34	296	35	218	36	11	37	61	39	6	41	66	45	1	47	16
CB01	52	31	53	408	54	3	56	28	57	12	59	47	60	16	62	21				
CB02	2	15	4	6	5	1	9	1	13	6	14	8	19	123	21	31	24	155	28	7
CB02	31	4	34	203	35	148	36	12	37	73	39	3	40	1	41	25	47	24	52	12
CB02	53	349	54	11	56	22	57	24	59	68	60	18	62	26						
CB03	2	7	4	26	13	124	14	120	19	23	21	3	24	241	25	48	26	19	31	10
CB03	34	408	35	232	37	29	41	32	45	1	47	36	51	12	52	24	53	237	54	1
CB03	56	18	59	62	60	307	61	113	62	45										
CB04	1	1	2	12	4	24	5	1	13	306	14	271	19	23	21	9	24	14	25	18
CB04	26	4	28	3	31	5	34	80	35	232	37	19	41	9	47	103	51	21	52	12
CB04	53	197	54	5	56	19	57	10	59	28	60	375	61	239	62	42				
CB05	4	2	8	1	13	20	14	25	25	180	26	5	28	3	34	110	35	50	37	15
CB05	40	4	51	20	53	80	61	35												
CB06	4	3	6	2	13	21	14	35	25	250	28	3	34	60	35	40	37	6	47	7
CB06	51	30	53	40	61	56	62	1												
CB07	13	68	14	45	19	10	25	264	28	8	34	55	35	22	36	2	37	11	47	40
CB07	52	8	53	33	54	1	56	16	57	1	60	9	61	38	62	10				
CB08	4	1	13	33	14	31	19	11	25	220	28	13	34	11	35	44	36	6	37	4
CB08	47	24	51	1	52	2	53	28	54	1	56	22	60	2	61	45	62	7		
SA01	19	1	52	3	53	81	54	3	56	6										
SA02	4	9	15	3	19	3	39	3	45	6	53	174	54	3	59	3				
SA03	1	39	4	3	29	12	31	12	33	6	39	3	40	3	45	12	48	6	50	3
SA03	53	378	54	3	56	18	59	15												
SA04	1	3	4	6	33	3	39	6	40	15	42	3	45	6	53	138	56	12	58	24
SA04	59	12																		

Appendix 1 cont:

SA05	2	72	15	6	19	51	27	15	33	900	42	123	43	12	46	3	49	15	53	156		
SA05	56	27	57	3	58	138	59	153	60	15	62	6										
SA06	2	6	33	33	44	3	53	24	56	6	59	33	62	3								
SA07	15	15	33	21	53	39	54	9	56	3	59	63	62	9								
SA08	15	36	29	3	33	6	47	15	53	186	54	30	56	3	59	39	62	6				
SA09	1	4	15	14	33	40	44	4	45	4	47	4	53	239	54	4	59	32				
SA10	1	26	2	5	3	3	4	8	5	5	7	2	8	2	12	2	15	2	19	2		
SA10	29	3	30	7	31	8	33	15	35	8	36	1	39	31	40	12	42	3	44	2		
SA10	45	41	46	1	52	3	53	425	54	13	55	2	56	21	57	2	59	23	62	6		
SA11	1	30	4	25	5	1	8	1	12	1	18	1	19	2	29	7	30	19	31	13		
SA11	33	13	35	6	36	2	39	26	40	9	42	1	44	1	45	78	46	5	47	2		
SA11	49	2	52	3	53	530	54	16	56	17	59	77	62	5								
SA12	1	13	3	1	4	26	5	1	7	1	17	1	18	2	19	4	27	39	29	12		
SA12	30	31	31	6	32	3	33	20	35	20	36	5	39	38	40	14	42	12	43	6		
SA12	45	32	46	1	49	1	50	7	52	3	53	408	56	63	57	3	58	2	59	37		
SA12	62	1																				
SA13	1	12	2	4	4	10	5	11	7	3	11	1	12	2	17	1	18	1	19	2		
SA13	29	4	31	12	32	2	33	33	35	16	36	4	39	31	40	45	42	14	43	3		
SA13	45	20	47	2	50	1	52	4	53	276	55	1	56	61	57	2	58	7	59	37		
SA13	62	3																				
SA14	4	1	8	1	31	1	35	2	39	4	40	6	42	23	43	2	49	1	50	1		
SA14	53	132	54	1	56	36	57	2	58	10	59	7	62	2								
SA15	1	4	4	2	29	2	31	1	35	3	39	4	40	4	42	8	43	5	45	1		
SA15	49	1	52	2	53	160	54	1	58	2	59	6	61	1	62	1						
SA16	4	1	35	1	36	28	39	1	42	6	43	3	46	2	47	5	48	1	49	2		
SA16	53	100	54	17	56	20	58	2	59	1	61	3	62	6								
SA17	29	1	36	12	39	1	40	3	42	16	43	2	46	1	47	3	49	1	53	90		
SA17	54	8	55	1	56	23	61	2														
SB01	4	1	31	2	32	1	35	2	45	1	52	4	53	120	56	11	58	4	59	6		
SB02	32	1	36	1	39	2	40	4	49	2	52	2	53	105	56	4	58	3	59	4		
SB03	12	4	36	20	45	1	47	4	49	2	52	2	53	60	54	2	56	5	58	3		
SB03	61	1	62	10																		
SB04	19	1	36	20	45	1	47	4	49	5	52	1	53	60	54	4	56	9	58	1		
SB04	62	6																				
SM01	1	8	2	46	3	2	4	6	5	2	10	1	13	1	19	6	30	24	31	5		
SM01	33	2	34	17	35	9	37	1	40	13	42	1	45	20	46	3	47	31	52	5		
SM01	53	532	54	45	56	50	59	200	60	2	62	5										
SM02	1	16	2	63	3	4	4	6	5	4	12	1	13	1	19	6	31	8	33	5		
SM02	34	11	35	10	37	4	40	7	42	1	45	43	52	13	53	460	54	35	56	39		
SM02	57	1	59	166																		
SM03	1	16	3	3	4	6	5	2	13	3	19	2	26	1	28	1	31	13	33	5		
SM03	35	10	36	1	37	1	40	27	42	8	43	1	44	1	45	19	46	1	48	1		
SM03	49	1	52	5	53	460	54	2	56	31	58	2	59	118	60	1	61	1	62	6		
SM04	1	16	3	2	4	6	5	1	11	1	12	1	13	4	19	2	31	6	35	9		
SM04	40	23	42	1	45	24	47	2	49	1	52	1	53	510	54	10	55	1	56	37		
SM04	58	7	59	95	62	2																

APPENDIX 2. Taxa abundances in soil samples on Islay. Taxa code numbers (Table 5.2) with corresponding abundance values are shown for each subsample (Table 5.1).

AA01	3	4	9	2	14	2	15	2	16	2	24	6								
AA02	3	2	5	10	16	1	23	1	28	2	34	1								
AA03	9	1	13	4	14	3	15	1	18	6	21	1	33	1						
AA04	12	1	24	1	2	1	30	1	33	2										
AA05	3	1	14	1	22	1	30	1	31	1	33	1								
AA06	9	1	14	1	16	2	18	10	24	1	31	1								
AA07	1	1	3	6	16	1	18	5	24	1	30	1	31	2						
AA08	4	74	18	12	22	1	33	4												
AA09	4	32	16	3	18	5	24	8	33	2										
AB01	3	1	6	1	16	3	18	23	28	3	2	1	33	2						
AB02	18	21	21	1	31	2	33	2												
AB03	17	1	18	6	31	1	33	1												
AB04	3	1	18	8	21	2	33	1												
AB05	18	7	33	1																
AB06	14	1	18	13																
AB07	3	2	4	21	14	1	16	1	18	11	24	4	28	2	33	1				
AB08	18	16	33	1																
AC01	3	1	5	25	13	1	18	9	29	1										
AC02	3	3	16	1	18	5	22	1	24	1	31	1	33	1						
AC03	14	3	18	2	33	1														
AC04	18	2	29	1																
AC05	3	1	9	1	18	12	24	2	31	1										
BB01	16	4	25	2	2	2	30	2												
BB02	8	1	9	1	10	1	11	1	16	6	18	1	24	2	26	1	28	19	2	1
BB02	30	1	32	1	33	1														
BB03	8	1	16	2	18	1	19	1	20	2	23	1	24	1	2	1	31	1	33	1
BB04	2	1																		
BB05	28	1	2	4	33	1														
BB06	16	1	30	1																
BB07	16	1	28	1																
BB08	30	1																		
BB09	16	1	18	1	20	1														
CW01	1	2	3	4	6	1	16	6	18	8	24	61	2	10	30	4	31	4		
CW02	1	1	3	2	4	1	16	4	18	8	24	22	28	3						
CW03	9	1	11	1	14	2	15	3	18	5	24	26	28	1	29	1				
CW04	24	12	30	1	33	2														
CW05	3	1	13	1	14	1	15	1	18	4	24	20	25	1	31	2				
CW06	11	1	18	6	24	7														
CW07	3	9	18	12	24	16	31	1												
CW08	3	3	16	1	18	4	24	1	25	1	33	1								
CW09	3	1	4	4	8	2	9	2	12	1	18	3	24	4	25	1	27	2	28	1
CW09	31	1																		
CW10	13	4	18	14	20	1	24	6	25	1	29	5	31	2						
CW11	18	7	24	16	29	1	33	2												
CW12	8	1	18	4	24	10														
CW13	8	2	18	11	20	1	24	4												
CW14	3	4	4	5	24	3	27	2	33	1										
SA01	1	2	7	6	12	2	16	2	18	6	19	2	20	16	21	4	28	6	2	2
SA01	30	2	31	6																
SA02	14	1	18	11	20	6	25	3	28	140	33	3								

Appendix 2 cont.:

SA03	8	2	16	3	18	5	20	7	28	51	30	3	31	1	32	1	33	2
SA04	1	2	14	1	20	5	28	3	2	2	31	1	33	1				
SA05	3	1	13	1	18	1	20	1	2	3	30	1	31	1				
SA06	18	10	28	89														
SA07	3	2	18	7	19	1	28	105	30	1								
SA08	18	15	20	4	25	1	28	64										
SA09	16	1	18	8	19	2	20	2	23	1	28	37						
SA10	1	1	7	1	16	1	18	14	19	1	20	10	30	1	31	1	33	8
SA11	18	2	20	4	33	4												
SA12	3	1	20	2	33	2												
SA13	18	3	20	1	28	6	34	1										
SA14	18	7	20	3	29	1												
SB01	18	1	20	2	32	1												
SB02	18	3																
SB03	4	52	18	5														
SM01	3	1	16	3	18	13	20	4	24	7	28	16	31	3	33	2		
SM02	3	1	14	1	16	3	18	2	20	6	24	4	33	1				

APPENDIX 3. Taxa abundances in the cow pats sampled on Islay. Taxa code numbers (Table 6.2) with corresponding abundance values are shown for each cow pat (Table 6.1).

A003	6	1	7	1	9	2	13	101	23	1	24	1	31	2	32	5	35	13	39	41
A003	45	135	47	24	48	3	51	2												
A004	1	57	9	3	18	1	20	2	21	2	33	1	34	1	39	101	45	4	47	3
A004	51	2																		
A005	13	40	20	1	23	2	33	1												
A006	20	1	23	1	48	1														
A007	6	7	12	6	24	1														
A008	6	1	12	1	36	1														
A009	26	1	38	1																
A010	6	1																		
A011	1	17	18	18	19	4	23	2	24	13	32	6	35	6	39	95	45	5	51	3
A012	13	2	20	1	21	1	24	5	26	2	35	10	39	93	45	1	51	1		
A013	50	1																		
A015	9	1	20	3	24	1	26	2	39	1	50	1	51	1						
A016	22	1	23	1	24	1	26	1												
A017	6	1	9	1	20	3	23	1	24	2	35	2	51	3						
A018	9	1	20	2	23	1	35	4	45	1	51	1	53	1						
A019	6	1	20	2	23	1	24	1	32	5	44	53	47	11	48	3	50	1	51	3
A020	17	1	26	1	31	1	32	4	37	2	39	3	42	1	44	1	50	5	51	14
A020	53	1																		
A021	6	1	7	3	50	1														
A022	7	1																		
A023	20	1	51	1																
A024	9	3	20	1	23	1	45	1												
A025	9	7	20	2	23	5	41	1	45	1	51	10								
A026	9	18	20	2	44	1														
A027	50	1																		
A029	9	6	31	1	35	1	50	5												
A030	9	5	31	1	50	4														
A031	9	10	22	1	50	1														
A032	9	18	31	1	45	8	47	26	50	1	51	16	52	17						
A033	9	21	20	49	24	1	31	1	32	1	37	2	45	2	51	5	52	6		
A034	20	2	31	1	32	1														
A035	47	1																		
A036	20	12	35	3	51	1														
A039	13	181	20	2	31	1	32	1	39	69	47	2	53	2						
A040	9	1	20	12	32	1	39	20												
A041	20	1																		
A043	20	22	24	1	39	169	40	5	44	1	45	2	47	37	51	2				
A044	7	1	13	508	39	29	47	5												
A045	36	2	42	6	54	3														
A046	9	11	53	1	54	1														
A047	9	1	13	65	50	3														
A048	7	3	13	1	53	1														
A050	13	4	24	1	53	1														
A051	6	1	12	1	42	3														
A052	13	1	24	1	53	2														
A053	2	3	6	16	13	1	24	1	31	3	35	2	53	1						
A054	6	1	7	3	13	1	20	12	31	2	47	2	51	4						
A055	6	3	15	1	38	1	42	1	47	1	50	1								
A056	6	4	32	1	35	1	39	20	44	10	46	12	47	1						
A057	6	1	9	2	26	1	31	1	41	3	44	5	51	7						
A058	24	1	35	6	53	2														
A059	6	1	9	1	44	8	45	34	53	3										
A060	10	8	11	3	31	2														

Appendix 3 cont:

A061	10	3	11	1	31	4
A062	9	1	32	1	51	3	53	1
A063	9	8	50	1	51	1
A065	51	1	53	1
A066	4	24	10	2	11	4	31	1	50	2
A067	2	4	9	1	24	2	31	1	39	142	42	121	47	11	48	3	51	1
A068	2	6	11	4	42	8	47	3
A069	2	49	4	27	10	2	11	2	20	2	24	1	31	2	32	2	42	29	47	48
A069	50	1
A070	6	1	9	3	24	7	32	1	39	248	40	81	44	1
A071	4	1	9	3	24	4	39	103	40	48	44	4	51	1
A072	24	3	42	14
A073	24	1	42	10
A074	9	2	20	1	24	4	31	1	37	3	39	94	51	2
A075	9	2	20	10	24	1	39	760	45	5
A076	1	8	9	3	24	1	45	2
A077	1	2	24	5	45	20
A078	9	1	24	1	42	1	44	1
A079	43	1
A080	24	2	51	1
A081	9	1	24	2	44	1	45	2
A082	24	1
A083	24	1	51	4
B001	24	1
B002	23	1
B003	20	7	24	1	39	15	47	8	50	1	54	83
B004	20	22	39	43	42	4	47	2	54	115
B005	20	18	24	8	32	3	36	2	39	29	45	8	50	2	51	2
B006	20	66	24	5	39	19	41	1	45	2	51	1
B007	12	1	24	1	25	2	53	1
B008	12	4	24	2	36	1
B009	20	5	23	1	24	3	39	2	50	1	51	3	53	1
B010	17	12	20	9	23	2	24	4	40	1	50	1	51	1	53	1
B011	17	5	18	2	25	2	27	1	31	1	32	6	41	2	50	2	53	10
B012	17	7	20	1	23	3	32	1	41	2	47	1	48	1	50	1
B013	3	11	6	1	12	9	24	2	31	14	32	1	50	13	53	1
B014	3	50	5	1	6	1	12	17	24	3	25	1	32	24	42	36	50	25
B015	50	1	51	1	53	3
B016	20	1	24	1	25	1	51	9	53	2
B017	20	11	23	1	24	4	26	20	39	13	40	10	41	1	51	25	53	1
B018	20	1	24	2	26	1	40	1	51	4
B019	5	1	31	1
B021	20	1	41	12	51	4
B022	20	16	23	5	24	1	30	1	32	1	39	7	41	1	51	5
B023	23	3	31	1	51	4
B025	45	3	51	10
B026	19	1	39	1
B027	10	2	31	9	50	18
B028	5	2	10	2	31	3	50	3
B029	9	11	18	4	24	2	31	1	32	1	39	1	45	41	47	3	51	6	52	5
B030	9	2	17	10	20	23	23	4	24	2	32	8	39	1	45	5	47	5	51	18
B031	20	1	23	1	39	5	40	1	41	2	50	1	51	3
B032	20	1	23	2	25	1	39	3	41	5	50	1	51	3
B033	23	1	31	2	50	3
B034	12	4	31	1	50	2
B035	20	7	24	1
B036	13	146	31	1	39	1
B037	18	1	20	1	23	1	24	3	32	2	39	69	45	1	53	1
B038	18	5	20	30	39	150	47	8

Appendix 3 cont:

B039 24 3 43 1
B040 24 1 32 1
B041 23 1 24 4 47 6 50 1
B042 12 1 24 1 45 1
B043 13 1
B044 8 1 9 3 31 1 32 17 39 20 46 3 47 4 50 7 51 15 52 23
B045 31 3 32 7 39 51 46 19 47 3 50 7 51 9 52 4
B046 43 1 47 3
B047 44 2 47 7 48 1 53 1
B048 2 9 10 2 25 1 39 27 46 60 47 72 51 1
B049 2 9 10 5 46 30 47 17 51 2
B050 9 6 20 4 23 7 32 4 51 2
B051 9 26 18 3 32 1 47 1 51 2
B052 24 4 42 45 47 2
B053 13 1 42 22
B054 42 36
B055 2 1 36 1 39 1 42 111 48 1
B056 1 5 24 6
B057 20 8 24 1 39 5
B058 24 7
B059 24 7
C001 24 1 35 8
C003 1 3 18 1 24 1 32 3 35 1 39 32 47 4
C004 24 2 32 10 39 195 45 1 51 2
C005 35 3 36 1 39 8 40 2 45 1 47 8
C006 16 1 17 2 45 1 47 1 50 1 54 1
C007 13 1
C009 35 1 42 6 44 1 43 4 47 36
C010 18 2 26 2 43 5 47 21 50 1
C011 20 1 23 1 26 3 32 1 35 4 43 2 45 1 47 4 49 1
C012 24 1 35 7
C013 3 1 6 2 12 1 31 2 35 1 42 1 50 2
C014 3 3 12 7 22 1 31 14 35 2 47 5 50 6
C015 44 5 50 2
C016 20 1 44 2
C017 9 15 24 2 32 1 35 28 39 1 40 1 45 2 47 17 51 3
C018 9 1 24 3 35 8 50 1
C019 6 1 47 1
C020 3 1 6 1 31 3 42 19 50 2
C021 15 1 24 1 35 2 43 2 45 2 50 1 51 4
C022 9 1 23 1 35 5 45 3 51 7
C023 9 45 20 12 23 1 29 1 35 2 39 2 51 2
C024 9 21 23 4 35 1 51 2
C026 35 1 47 8 50 2
C027 9 4 20 38 26 7 31 1 32 3 35 10 45 3 50 1 51 8
C028 9 5 23 1 31 2 35 1 50 1
C029 24 2 35 3 43 7 46 1 51 1
C030 6 2 9 4 26 1 43 9
C031 28 7 35 2 43 2
C032 9 8 50 1
C033 9 2
C034 24 1 35 1
C035 9 1 18 1 20 9 24 1 47 1
C036 20 8 45 1 47 3
C037 22 1 24 3 35 3
C040 3 1 20 1 36 2 47 62 51 1
C041 23 1 31 5 42 11 47 32
C042 6 1 12 1 31 1 35 2 39 2 42 94 47 43
C043 9 1 24 1 42 223 44 23 47 1

Appendix 3 cont:

C044	42	6	44	3	47	3														
C045	24	1	35	5	38	1														
C046	21	1	23	2	35	5	36	1	38	1										
C047	24	1	31	1	32	7	35	1	46	1	47	2	50	9						
C048	2	9	5	1	6	3	9	4	32	4	35	6	39	2	46	60	47	6	50	3
C048	51	9																		
C049	6	1	9	6	24	3	35	36	44	6	50	1								
C050	6	1	35	27	44	3	50	1												
C051	43	3	45	1	50	2	51	1	52	1										
C052	9	34	20	26	24	1	39	3	43	18	45	3	51	7						
C053	28	1	44	5	50	1														
C054	15	1	24	1	28	4	50	2												
C057	4	1	35	2	51	1														
C058	4	1	35	2	51	1														
C059	4	1	39	5	42	8	44	1	47	10										
C060	4	2	39	3	42	12	47	21												
C061	24	1	35	2	39	37	45	2												
C062	35	2	39	36																
C063	24	2	35	2	39	37	45	8	50	1										
C064	1	1	9	2	24	3	35	2	39	105										
S001	22	1	23	2	24	3	25	1	26	1										
S002	34	1	45	1																
S003	16	2	24	2	32	2	34	1	39	27	41	1	42	1	47	8	48	1	51	1
S003	54	2																		
S004	14	1	32	1	39	11	42	45	45	2	54	16								
S005	23	1	24	3	25	1	45	1	53	1										
S006	25	1																		
S007	20	2	23	1	24	1	32	3	45	1	54	7								
S008	23	1	24	1	32	3	40	1	45	17										
S009	12	1	24	2	25	4	32	3	41	1	45	2	47	7	54	1				
S010	20	3	23	1	24	2	25	3	45	318	47	32	54	1						
S011	17	3	20	5	23	1	24	3	25	2	39	1	40	1	41	2	48	1	51	5
S012	24	7	40	1	50	1	51	2												
S013	12	1	23	2	24	1	50	1												
S014	23	2	24	2	32	1	39	3	50	1										
S015	9	10	25	1	34	1														
S016	9	3	23	1	25	2	31	2												
S017	9	10	25	2	39	1														
S018	20	3	23	1	32	2	39	13	42	152	44	1	54	2						
S019	20	26	24	2	39	293	42	22	44	1	47	2	54	2						
S022	14	1	24	1	25	1	54	37												
S023	15	1	24	1																

APPENDIX 4. Taxa abundances in chough faeces. Taxa code numbers (Table 7.2) with corresponding abundance values are shown for each subsample (Table 7.1).

R35A	7	1	8	1	11	95	12	1	13	10	15	1	18	1	21	4	24	1	27	2	28	1	30	2
R35A	38	6	44	1	46	1	47	1	49	5	50	1
R35B	8	1	11	67	13	7	18	2	19	1	21	2	24	2	28	1	30	1	34	1	38	10	46	1
R35B	47	1	49	5
W1A	1	1	4	29	21	1	22	10	27	1	30	2	34	7	44	1	45	1	47	8	48	1	50	1
W1B	1	2	4	12	14	2	21	1	22	14	24	1	27	1	30	2	34	4	37	1	47	17	48	1
W1B	50	2
R71A	5	1	7	1	11	2	17	100	22	3	26	50	27	1	28	1	31	2	47	24
R71B	11	1	14	1	17	60	22	7	26	50	28	1	31	3	42	1	47	14	50	1
R71C	1	1	6	1	11	1	17	5	21	1	22	1	23	1	24	1	26	50	31	1	36	3	43	1
R71C	44	1	46	1	47	2
R71D	4	1	11	2	14	1	17	5	20	1	21	1	22	1	26	50	27	2	30	1	36	2	44	1
R71D	46	1	47	6	50	2
R71E	1	5	4	1	5	2	7	4	11	2	14	1	15	1	21	1	22	1	27	1	28	1	30	1
R71E	34	2	38	1	47	14	50	1
R71F	1	3	5	3	11	8	14	2	17	1	23	1	24	1	28	1	30	1	34	1	38	2	44	2
R71F	47	7
R71G	4	9	6	3	9	1	11	16	12	2	17	1	21	1	26	50	27	3	28	1	34	2	38	1
R71G	46	1	47	4	50	1
R71H	2	1	4	13	6	3	11	7	12	2	26	50	27	5	28	1	34	1	46	1	47	3
R71I	6	1	11	1	17	1	21	3	26	50	27	2	32	1	36	8	37	1	45	1	47	1
R71J	17	1	21	2	26	50	27	4	31	1	36	6	37	4
R71K	1	1	17	300	21	1	22	5	26	20	30	1	33	1	36	2	47	18	50	2
R71L	4	1	11	3	17	300	20	1	21	2	22	11	26	20	27	1	31	1	33	1	34	1	44	1
R71L	47	28
R71M	1	1	2	1	11	2	14	10	17	50	21	2	22	1	26	50	27	1	29	1	31	1	44	2
R71M	46	1	47	6	50	1
R71N	10	1	11	15	17	20	21	1	22	2	26	50	29	1	31	1	34	1	44	2	46	1	47	8
R71N	50	1
R71O	1	1	7	1	8	1	12	1	14	1	18	1	21	2	22	1	25	1	27	1	28	1	30	1
R71O	34	1	40	2	44	2	45	1	47	11
R71P	1	2	7	1	8	2	17	10	18	2	21	2	24	2	25	1	28	1	30	1	34	1	39	1
R71P	44	3	45	3	47	19
R71Q	1	3	4	1	5	3	21	1	23	1	24	1	26	20	27	1	30	2	34	3	39	1	44	2
R71Q	47	11	50	6
R71R	1	2	23	1	26	20	30	2	34	15	39	1	44	1	47	14	50	3
E6A	6	9	7	1	11	6	12	2	21	4	22	1	28	1	30	1	40	1	46	5	47	1	48	1
E6A	49	50
E6B	6	6	7	1	11	8	12	1	14	1	21	5	22	2	27	1	28	1	30	1	46	5	47	3
E6B	48	1	49	50
E6C	1	2	7	1	8	1	12	1	18	4	28	1	30	2	36	1	47	8
E6D	1	2	7	2	8	4	18	1	23	1	24	1	28	1	36	5	42	1	47	7
E19A	7	1	8	1	18	4	21	1	22	2	23	3	28	1	30	1	45	4	46	1	47	9	48	1
E19B	7	1	18	2	19	1	21	1	23	2	28	1	40	1	45	3	46	1	47	6	48	1
R25A	7	1	8	2	14	1	18	2	34	1	41	1	45	1	47	2	48	1
R25B	7	1	8	1	14	3	18	9	34	1	45	2	47	7	48	1
R5A	5	1	7	1	11	3	12	1	21	2	23	1	24	1	30	3	34	32	47	5
R5B	1	1	5	1	7	1	11	2	23	1	30	3	34	18	44	1	45	1	47	4	50	1
R67A	7	1	8	1	21	2	23	1	34	17	36	10	40	1	47	5

Appendix 4 cont:

R67B	7	2	21	2	23	2	34	12	36	16	40	1	45	1	47	6						
R7A	1	1	22	1	27	1	30	1	39	1	42	17	43	2	47	26						
R7B	22	2	27	2	30	3	34	1	37	1	39	1	42	4	45	2	47	35				
E13A	7	1	8	2	23	1	27	1	30	1	34	4	36	13	40	1	45	2	47	3		
E13B	7	1	8	3	21	2	23	1	27	1	30	4	34	2	36	36	40	1	45	1	47	3
R1A	14	2	17	2	21	4	22	4	26	50	27	2	28	1	29	1	30	3	45	5		
R1B	10	1	14	1	17	1	21	6	22	11	26	50	27	2	28	1	29	1	30	4	31	2	45	3
R1B	47	1																				
R1C	4	1	6	1	17	3	21	1	26	50	30	2	36	1	47	5	48	1				
R1D	4	2	6	1	17	13	22	2	26	50	27	1	29	1	30	1	37	1	42	1	47	6	48	1
R24A	3	1	4	3	11	11	14	6	21	4	22	1	26	50	27	12	30	1	31	5	34	1	36	18
R24A	37	8	44	1	45	1	46	1	47	1	48	1										
R24B	3	3	4	2	11	7	14	11	17	1	21	1	22	3	26	50	27	18	30	1	31	1	34	1
R24B	36	12	37	5	44	2	45	1	46	1	47	5	50	2								
R24C	14	40	17	1	21	1	22	21	26	5	27	1	28	1	29	1	30	5	31	1	44	2	45	6
R24C	47	4	50	1																		
R24D	4	1	14	75	17	4	21	1	22	15	26	5	27	1	28	1	29	1	30	5	31	1	37	3
R24D	44	1	45	4	47	3	50	1														
E18A	6	3	11	3	12	1	21	3	22	4	26	5	27	21	35	13	36	2	37	2	43	1	47	2
E18A	48	1																				
E18B	6	1	11	6	21	1	22	2	26	5	27	8	31	1	35	24	36	17	37	6	42	1	45	1
E18B	47	3	48	1																		
E18C	3	6	12	1	22	47	27	1	29	1	31	1	43	14	44	1	45	2	47	120		
E18D	1	1	21	1	22	68	27	2	29	1	31	4	43	5	44	1	45	4	47	85		
R69A	7	1	21	1	22	1	23	1	30	1	45	1	46	2	47	10	48	1				
R69B	8	1	23	1	44	1	45	1	46	3	47	8	48	1	50	1						
R31A	5	3	7	6	10	1	22	2	27	1	28	1	30	2	45	2	47	7				
R31B	1	1	5	2	7	11	10	1	12	1	16	1	22	2	23	2	25	1	27	1	28	1	44	1
R31B	45	6	47	9	48	1																
E11A	6	1	8	1	11	1	17	1	21	4	22	1	26	50	27	1	28	1	29	1	30	2	46	1
E11A	47	3																				
E11B	6	2	7	1	11	3	12	1	17	1	21	1	22	2	26	50	27	2	30	2	31	1	45	1
E11B	46	1	47	5																		
R53A	5	1	7	2	8	1	9	5	10	1	11	22	18	1	21	1	27	1	28	1	30	7	34	1
R53A	36	1	39	1	45	1	46	1	47	2												
R53B	7	1	8	3	9	3	10	1	11	17	27	1	28	1	30	1	34	1	36	2	46	1	47	1
E21A	17	1	21	2	22	4	26	50	27	1	29	1	47	3	50	2						
E21B	21	1	22	2	26	50	29	4	47	6	50	1										

APPENDIX 5. Taxa abundances in the dung of each of the experimental cow pats. Taxa numbers (Table 8.2) with corresponding abundance values are shown for each pat number (Table 8.1).

001	19	1	32	3	35	2	36	5	37	39	42	1	48	2
001	53	63	54	2	55	5								
002	32	14	36	1	37	19	43	1	44	1	53	35	55	1
003	25	1	32	12	35	3	36	1	37	10	42	1	48	1
003	50	1	53	19	55	5								
004	36	1	37	4	44	1	53	10						
005	32	2	35	2	36	1	37	16	42	2	49	1	53	14
005	54	1	55	1										
006	03	1	25	1	32	25	35	1	37	9	38	2	42	1
006	53	19	55	3	58	2								
007	32	5	36	4	37	26	42	4	49	2	53	49	54	3
007	55	7												
008	03	3	42	1	49	1	53	12	54	1	58	1		
009	03	2	29	3	32	6	37	4	42	1	51	1	53	17
009	55	5												
010	01	1369	02	60	06	10	23	56	24	1	29	63	31	6
010	32	25	35	1	37	9	38	3	53	30	54	1	55	2
011	01	732	02	82	04	6	06	12	23	9	24	1	29	109
011	30	2	31	2	32	39	37	12	38	1	42	8	49	1
011	53	42	54	3	55	4								
012	01	213	02	44	04	1	05	7	19	1	29	40	31	1
012	32	8	37	10	38	2	42	4	53	28	54	1		
013	01	1	06	9	17	3	32	24	36	4	37	3	40	1
013	53	14	54	5										
014	06	9	17	12	19	1	22	1	29	1	32	15	36	3
014	53	7	54	2	60	1	61	1	63	1				
015	06	2	16	1	17	2	31	3	32	18	35	1	36	2
015	50	2	53	6	54	6								
016	06	1	32	4	35	1	37	2	42	1	53	6	54	3
016	60	1												
017	06	9	08	1	32	26	53	6	54	7				
018	06	1	17	3	32	31	36	1	37	1	43	1	51	1
018	53	5	54	8										
019	32	3	53	6	54	2	64	2						
020	32	36	36	2	53	3	54	1						
021	06	1	17	4	19	1	32	23	36	2	37	2	42	1
021	43	2	48	1	53	8	54	2						
022	01	31	02	2	04	1	06	3	08	10	17	8	23	17
022	29	15	32	54	42	2	54	1						
023	01	81	02	1	06	12	08	17	23	44	27	25	29	19
023	31	7	32	56	37	3	42	1	43	2	54	5		
024	01	78	02	5	04	2	06	3	08	103	17	7	23	40
024	27	63	29	8	31	1	32	10	37	4	53	2	54	22
025	06	2	10	1	17	2	26	1	32	2	35	1	36	3
026	06	1	17	1	32	17	35	1	53	3				
027	06	28	17	2	32	12	36	2	50	1	53	2	64	2
027	65	1												
028	06	1	17	2	32	14	53	1						
029	17	2	32	21	53	1	54	1	64	4				
030	17	1	32	5	54	1								
031	17	2	32	37	36	11	53	2						
032	17	2	32	8	54	1	64	2						
033	06	5	17	1	32	6								
034	32	6	54	1										
035	08	1	17	6	27	2	29	2	31	3	32	5		
036	17	6	23	1	29	1	32	32	54	1	64	1		

Appendix 5 cont:

037	06	2	17	5	19	2	32	4	43	1	64	1		
038	10	2	17	2	28	1	32	2	35	1	36	2	53	1
038	64	3												
039	06	1	32	2	35	1	36	8	40	1	54	2	65	1
040	06	1	17	1	35	1	36	1	54	1	64	2		
041	32	6	53	4	54	3								
042	32	20	53	1	54	1								
043	06	1	32	1	53	2	64	3						
044	07	2	32	4	54	1								
045	06	5	07	7	32	12	35	1	36	3	54	1		
046	06	2	24	1	26	1	32	4	43	1	64	1		
047	32	10	35	1	54	5	64	2						
048	06	5	32	14										
049	63	2												
050	33	1	63	8										
051	32	1	63	8										
055	32	1	33	1	53	1	63	4						
056	63	2												
058	65	1												
059	63	7												
061	07	4	10	3	32	19	43	3	53	30				
062	17	4	36	1	37	1	43	6	46	1	53	56	54	3
063	36	1	44	1	53	14								
064	17	25	32	7	53	4								
065	01	10	07	2	10	3	17	10	23	2	32	4	35	1
065	43	1	46	1	53	18								
066	07	2	17	6	32	10	43	2	44	1	53	21		
067	01	13	07	30	10	5	17	20	23	6	29	2	31	1
067	32	32	42	1	53	76	54	1						
068	01	5	02	1	07	35	10	3	17	2	32	21	53	11
069	01	1	07	62	10	1	17	4	29	1	31	1	32	12
069	43	2	53	12										
070	01	277	02	40	04	2	07	124	12	17	17	10	18	1
070	23	66	29	46	32	22	53	23						
071	02	182	04	6	07	19	12	10	16	1	17	11	24	1
071	29	18	30	6	32	9	35	1	43	2	53	9		
072	01	14	02	9	04	3	07	101	12	14	17	4	23	1
072	24	4	29	8	32	20	42	1	53	86				
073	06	1	07	1	20	4	31	1	32	2	43	2	46	1
073	53	2	54	4	63	3								
074	06	20	07	29	18	1	32	2	35	1	43	4	53	4
074	54	5	63	1										
075	06	9	07	11	43	4	53	1						
076	06	18	07	41	20	1	32	2	43	5	46	1		
077	06	6	32	6	43	2	53	1						
078	07	15	16	1	18	1	32	22	43	1	54	2		
079	06	4	07	18	29	1	31	2	32	4	43	1	46	1
079	53	3	54	2										
080	06	1	07	5	32	12	43	3						
081	06	1	07	65	08	1	32	2	43	2	63	1		
082	01	51	04	2	07	135	17	4	23	2	32	2	35	1
082	46	1												
083	01	29	02	2	06	2	23	8	46	1	53	2	54	1
083	63	1												
084	01	48	02	1	04	4	06	6	07	84	12	1	17	2
084	18	1	23	25	32	2	35	2	43	1	53	4	54	1
084	63	3												
085	07	3	32	1	43	2	53	1	63	5				
086	07	4	53	1	63	1								

Appendix 5 cont:

087	07	11	46	1	53	2	63	8						
088	07	12	32	3	53	1	63	7						
089	07	8	31	2	63	3								
090	07	1	32	1	53	1	65	1						
091	07	89	43	1	57	1	63	5						
092	07	16	32	4	53	1	63	8						
093	07	33	18	1	32	6	43	3	53	2	63	1		
094	07	2	63	2										
097	07	3	63	5										
101	07	1	63	1										
121	01	55	03	7	06	2	10	4	23	34	28	2	29	2
121	32	2	36	1	37	2	43	1	46	1	53	4	63	1
122	10	19	28	1	32	43	37	9	43	5	53	12		
123	01	5	03	1	06	1	10	5	23	2	32	17	37	4
123	38	1	43	2	53	12								
124	01	4	03	4	06	1	10	9	23	1	29	1	32	23
124	37	7	42	2	46	1	53	6						
125	01	2	06	2	07	5	10	1	28	2	31	4	32	6
125	43	5	52	2	53	10								
126	01	198	03	5	06	1	08	1	10	7	13	1	23	24
126	29	2	31	1	32	18	37	6	42	1	43	1	53	5
127	01	53	03	11	05	1	06	2	07	1	10	4	17	1
127	23	21	28	2	31	1	32	9	42	1	53	8		
128	01	11	03	37	08	1	10	1	23	4	28	1	29	1
128	43	2	53	4										
129	01	24	03	16	06	2	10	24	23	25	28	6	29	2
129	32	14	36	1	37	1	43	1	53	2	63	1		
130	01	270	02	202	04	27	07	2	08	53	12	1	23	143
130	27	26	28	2	29	23	32	3	35	1	37	3	43	1
130	53	1												
131	01	544	02	388	04	77	05	2	06	3	07	9	08	55
131	11	10	23	152	27	2	29	26	31	1	32	2	37	3
131	43	3	53	4	63	1								
132	01	308	02	71	04	7	05	4	06	1	07	5	08	19
132	10	3	14	1	23	92	29	62	32	6	37	10	38	2
132	53	5												
133	06	14	08	1	42	1	43	1	63	3				
134	06	46	07	1	08	9	09	11	10	1	29	1	32	20
134	43	2	53	1	63	2								
135	01	10	06	27	08	34	23	5	37	1	43	5	53	1
135	63	2												
139	01	1	06	24	07	3	08	1	32	2	36	1	43	2
139	46	1	53	2	63	2								
140	01	9	06	12	08	41	29	3	32	1	43	1	63	2
142	01	481	06	139	07	3	08	79	11	4	23	16	29	11
142	31	1	43	2	54	1	63	4						
143	01	224	02	3	06	33	08	46	11	4	21	1	23	3
143	29	1	31	3	53	1	63	5						
144	01	598	02	2	04	7	05	14	06	12	08	34	09	2
144	11	4	23	106	31	3	32	6	37	1	42	1	43	2
144	53	2	54	2	63	6								
145	01	1	06	14	08	2	29	1	33	1	46	3	63	2
146	06	23	08	3	21	1	29	1	47	1	53	1	63	4
147	06	8	08	2	43	1	49	1	63	2				
150	01	14	06	30	08	135	27	1	29	1	43	3	46	1
151	01	103	06	2	07	10	08	209	19	1	23	1	29	1
151	31	2	46	1	63	2								
152	31	1	63	3										
154	01	1555	04	5	06	97	08	237	11	5	19	5	21	1

Appendix 5 cont:

154	22	2	23	12	29	2	43	3	63	1				
181	49	1												
182	03	1	33	1										
184	46	1												
185	46	1	49	1										
186	17	4	36	1	41	1	46	2	49	1	53	2		
187	01	9	03	18	37	1	49	3	53	1				
189	01	1	03	1	35	1	38	1	43	1	46	2	49	10
190	01	209	03	861	04	9	21	1	23	9	38	1	40	2
190	47	1	49	3	53	3	63	1						
191	01	5	03	2962	11	9	15	16	23	1	47	1	53	2
192	01	6	03	693	11	8	15	9	40	1	43	1	53	2
193	01	1	03	2	06	9	11	1	63	5				
194	01	4	06	2	08	4	10	6	19	1	46	1	63	1
195	01	3	06	8	08	7	63	1						
196	01	20	03	4	06	10	08	3	10	4	29	5	46	5
196	63	2												
197	01	4	06	10	07	1	08	9	10	3	19	2	63	1
198	01	1	06	1	07	1	08	2	10	1	46	3	63	8
199	01	3	06	31	08	2	10	1	29	1	46	1	53	1
199	63	1												
200	01	51	06	29	08	2	10	14	19	1	53	1	63	1
201	01	14	06	18	08	9	09	2	19	3	29	2	46	1
201	53	2												
202	01	489	06	26	08	29	10	1	11	3	19	1	23	6
202	29	2	33	1	63	3								
203	01	602	05	36	06	43	08	96	16	1	23	6	29	10
203	63	1												
204	01	1429	04	27	05	209	08	393	10	5	23	1	29	5
204	46	3	53	2	63	1								
205	06	11	10	1	11	1	19	2	46	17	47	2	63	2
206	06	23	46	4	63	2								
207	01	1	06	6	08	17	32	1	46	1	53	2	63	1
208	06	11	08	10	29	1	63	2						
209	07	1	63	3										
210	01	3	06	10	08	61	09	5	19	1	23	2	46	1
210	53	4	63	1										
211	03	1	19	6	46	1	63	10						
212	01	50	03	3	06	39	08	78	10	4	21	1	29	4
212	43	1	46	1	53	2	63	2						
214	01	86	06	55	08	403	17	8	19	1	23	1	29	2
214	33	1	46	3	63	5								
215	01	198	05	13	06	6	08	301	16	1	17	16	19	1
215	21	1	22	6	29	1	32	3	33	1	46	2	63	2
216	01	46	05	55	06	4	08	315	17	1	19	2	22	7
216	29	5	32	1	46	2	53	2	63	2				

APPENDIX 6. Environmental variables used in the CANOCO analysis of taxa abundances in the dung of the experimental cow pats (Appendix 5). See p.195 for explanation of columns.

001	1	1	5	1	6	15	7	1	8	227	9	3	10	137
002	1	1	5	2	6	15	7	1	8	227	9	3	10	137
003	1	1	5	3	6	15	7	1	8	227	9	3	10	137
004	1	1	5	1	6	15	7	2	8	227	9	3	10	137
005	1	1	5	2	6	15	7	2	8	227	9	3	10	137
006	1	1	5	3	6	15	7	2	8	227	9	3	10	137
007	1	1	5	1	6	15	7	3	8	227	9	3	10	137
008	1	1	5	2	6	15	7	3	8	227	9	3	10	137
009	1	1	5	3	6	15	7	3	8	227	9	3	10	137
010	1	1	5	1	6	15	7	4	8	227	9	3	10	137
011	1	1	5	2	6	15	7	4	8	227	9	3	10	137
012	1	1	5	3	6	15	7	4	8	227	9	3	10	137
013	1	1	5	1	6	30	7	1	8	453	9	48	10	244
014	1	1	5	2	6	30	7	1	8	453	9	48	10	244
015	1	1	5	3	6	30	7	1	8	453	9	48	10	244
016	1	1	5	1	6	30	7	2	8	453	9	48	10	244
017	1	1	5	2	6	30	7	2	8	453	9	48	10	244
018	1	1	5	3	6	30	7	2	8	453	9	48	10	244
019	1	1	5	1	6	30	7	3	8	453	9	48	10	244
020	1	1	5	2	6	30	7	3	8	453	9	48	10	244
021	1	1	5	3	6	30	7	3	8	453	9	48	10	244
022	1	1	5	1	6	30	7	4	8	453	9	48	10	244
023	1	1	5	2	6	30	7	4	8	453	9	48	10	244
024	1	1	5	3	6	30	7	4	8	453	9	48	10	244
025	1	1	5	1	6	45	7	1	8	705	9	54	10	400
026	1	1	5	2	6	45	7	1	8	705	9	54	10	400
027	1	1	5	3	6	45	7	1	8	705	9	54	10	400
028	1	1	5	1	6	45	7	2	8	705	9	54	10	400
029	1	1	5	2	6	45	7	2	8	705	9	54	10	400
030	1	1	5	3	6	45	7	2	8	705	9	54	10	400
031	1	1	5	1	6	45	7	3	8	705	9	54	10	400
032	1	1	5	2	6	45	7	3	8	705	9	54	10	400
033	1	1	5	3	6	45	7	3	8	705	9	54	10	400
034	1	1	5	1	6	45	7	4	8	705	9	54	10	400
035	1	1	5	2	6	45	7	4	8	705	9	54	10	400
036	1	1	5	3	6	45	7	4	8	705	9	54	10	400
037	1	1	5	1	6	60	7	1	8	991	9	67	10	476
038	1	1	5	2	6	60	7	1	8	991	9	67	10	476
039	1	1	5	3	6	60	7	1	8	991	9	67	10	476
040	1	1	5	1	6	60	7	2	8	991	9	67	10	476
041	1	1	5	2	6	60	7	2	8	991	9	67	10	476
042	1	1	5	3	6	60	7	2	8	991	9	67	10	476
043	1	1	5	1	6	60	7	3	8	991	9	67	10	476
044	1	1	5	2	6	60	7	3	8	991	9	67	10	476
045	1	1	5	3	6	60	7	3	8	991	9	67	10	476
046	1	1	5	1	6	60	7	4	8	991	9	67	10	476
047	1	1	5	2	6	60	7	4	8	991	9	67	10	476
048	1	1	5	3	6	60	7	4	8	991	9	67	10	476
049	1	1	5	1	6	90	7	1	8	1527	9	187	10	608
050	1	1	5	2	6	90	7	1	8	1527	9	187	10	608

Appendix 6 cont:

051	1	1	5	3	6	90	7	1	8	1527	9	187	10	608
052	1	1	5	1	6	90	7	2	8	1527	9	187	10	608
053	1	1	5	2	6	90	7	2	8	1527	9	187	10	608
054	1	1	5	3	6	90	7	2	8	1527	9	187	10	608
055	1	1	5	1	6	90	7	3	8	1527	9	187	10	608
056	1	1	5	2	6	90	7	3	8	1527	9	187	10	608
057	1	1	5	3	6	90	7	3	8	1527	9	187	10	608
058	1	1	5	1	6	90	7	4	8	1527	9	187	10	608
059	1	1	5	2	6	90	7	4	8	1527	9	187	10	608
060	1	1	5	3	6	90	7	4	8	1527	9	187	10	608
061	2	1	5	1	6	15	7	1	8	286	9	13	10	76
062	2	1	5	2	6	15	7	1	8	286	9	13	10	76
063	2	1	5	3	6	15	7	1	8	286	9	13	10	76
064	2	1	5	1	6	15	7	2	8	286	9	13	10	76
065	2	1	5	2	6	15	7	2	8	286	9	13	10	76
066	2	1	5	3	6	15	7	2	8	286	9	13	10	76
067	2	1	5	1	6	15	7	3	8	286	9	13	10	76
068	2	1	5	2	6	15	7	3	8	286	9	13	10	76
069	2	1	5	3	6	15	7	3	8	286	9	13	10	76
070	2	1	5	1	6	15	7	4	8	286	9	13	10	76
071	2	1	5	2	6	15	7	4	8	286	9	13	10	76
072	2	1	5	3	6	15	7	4	8	286	9	13	10	76
073	2	1	5	1	6	30	7	1	8	558	9	78	10	133
074	2	1	5	2	6	30	7	1	8	558	9	78	10	133
075	2	1	5	3	6	30	7	1	8	558	9	78	10	133
076	2	1	5	1	6	30	7	2	8	558	9	78	10	133
077	2	1	5	2	6	30	7	2	8	558	9	78	10	133
078	2	1	5	3	6	30	7	2	8	558	9	78	10	133
079	2	1	5	1	6	30	7	3	8	558	9	78	10	133
080	2	1	5	2	6	30	7	3	8	558	9	78	10	133
081	2	1	5	3	6	30	7	3	8	558	9	78	10	133
082	2	1	5	1	6	30	7	4	8	558	9	78	10	133
083	2	1	5	2	6	30	7	4	8	558	9	78	10	133
084	2	1	5	3	6	30	7	4	8	558	9	78	10	133
085	2	1	5	1	6	45	7	1	8	822	9	133	10	208
086	2	1	5	2	6	45	7	1	8	822	9	133	10	208
087	2	1	5	3	6	45	7	1	8	822	9	133	10	208
088	2	1	5	1	6	45	7	2	8	822	9	133	10	208
089	2	1	5	2	6	45	7	2	8	822	9	133	10	208
090	2	1	5	3	6	45	7	2	8	822	9	133	10	208
091	2	1	5	1	6	45	7	3	8	822	9	133	10	208
092	2	1	5	2	6	45	7	3	8	822	9	133	10	208
093	2	1	5	3	6	45	7	3	8	822	9	133	10	208
094	2	1	5	1	6	45	7	4	8	822	9	133	10	208
095	2	1	5	2	6	45	7	4	8	822	9	133	10	208
096	2	1	5	3	6	45	7	4	8	822	9	133	10	208
097	2	1	5	1	6	60	7	1	8	1110	9	198	10	265
098	2	1	5	2	6	60	7	1	8	1110	9	198	10	265
099	2	1	5	3	6	60	7	1	8	1110	9	198	10	265
100	2	1	5	1	6	60	7	2	8	1110	9	198	10	265
101	2	1	5	2	6	60	7	2	8	1110	9	198	10	265
102	2	1	5	3	6	60	7	2	8	1110	9	198	10	265
103	2	1	5	1	6	60	7	3	8	1110	9	198	10	265

Appendix 6 cont:

104	2	1	5	2	6	60	7	3	8	1110	9	198	10	265
105	2	1	5	3	6	60	7	3	8	1110	9	198	10	265
106	2	1	5	1	6	60	7	4	8	1110	9	198	10	265
107	2	1	5	2	6	60	7	4	8	1110	9	198	10	265
108	2	1	5	3	6	60	7	4	8	1110	9	198	10	265
109	2	1	5	1	6	90	7	1	8	1627	9	313	10	382
110	2	1	5	2	6	90	7	1	8	1627	9	313	10	382
111	2	1	5	3	6	90	7	1	8	1627	9	313	10	382
112	2	1	5	1	6	90	7	2	8	1627	9	313	10	382
113	2	1	5	2	6	90	7	2	8	1627	9	313	10	382
114	2	1	5	3	6	90	7	2	8	1627	9	313	10	382
115	2	1	5	1	6	90	7	3	8	1627	9	313	10	382
116	2	1	5	2	6	90	7	3	8	1627	9	313	10	382
117	2	1	5	3	6	90	7	3	8	1627	9	313	10	382
118	2	1	5	1	6	90	7	4	8	1627	9	313	10	382
119	2	1	5	2	6	90	7	4	8	1627	9	313	10	382
120	2	1	5	3	6	90	7	4	8	1627	9	313	10	382
121	3	1	5	1	6	15	7	1	8	288	9	65	10	57
122	3	1	5	2	6	15	7	1	8	288	9	65	10	57
123	3	1	5	3	6	15	7	1	8	288	9	65	10	57
124	3	1	5	1	6	15	7	2	8	288	9	65	10	57
125	3	1	5	2	6	15	7	2	8	288	9	65	10	57
126	3	1	5	3	6	15	7	2	8	288	9	65	10	57
127	3	1	5	1	6	15	7	3	8	288	9	65	10	57
128	3	1	5	2	6	15	7	3	8	288	9	65	10	57
129	3	1	5	3	6	15	7	3	8	288	9	65	10	57
130	3	1	5	1	6	15	7	4	8	288	9	65	10	57
131	3	1	5	2	6	15	7	4	8	288	9	65	10	57
132	3	1	5	3	6	15	7	4	8	288	9	65	10	57
133	3	1	5	1	6	30	7	1	8	548	9	117	10	112
134	3	1	5	2	6	30	7	1	8	548	9	117	10	112
135	3	1	5	3	6	30	7	1	8	548	9	117	10	112
136	3	1	5	1	6	30	7	2	8	548	9	117	10	112
137	3	1	5	2	6	30	7	2	8	548	9	117	10	112
138	3	1	5	3	6	30	7	2	8	548	9	117	10	112
139	3	1	5	1	6	30	7	3	8	548	9	117	10	112
140	3	1	5	2	6	30	7	3	8	548	9	117	10	112
141	3	1	5	3	6	30	7	3	8	548	9	117	10	112
142	3	1	5	1	6	30	7	4	8	548	9	117	10	112
143	3	1	5	2	6	30	7	4	8	548	9	117	10	112
144	3	1	5	3	6	30	7	4	8	548	9	117	10	112
145	3	1	5	1	6	45	7	1	8	805	9	180	10	174
146	3	1	5	2	6	45	7	1	8	805	9	180	10	174
147	3	1	5	3	6	45	7	1	8	805	9	180	10	174
148	3	1	5	1	6	45	7	2	8	805	9	180	10	174
149	3	1	5	2	6	45	7	2	8	805	9	180	10	174
150	3	1	5	3	6	45	7	2	8	805	9	180	10	174
151	3	1	5	1	6	45	7	3	8	805	9	180	10	174
152	3	1	5	2	6	45	7	3	8	805	9	180	10	174
153	3	1	5	3	6	45	7	3	8	805	9	180	10	174
154	3	1	5	1	6	45	7	4	8	805	9	180	10	174
155	3	1	5	2	6	45	7	4	8	805	9	180	10	174
156	3	1	5	3	6	45	7	4	8	805	9	180	10	174

Appendix 6 cont:

157	3	1	5	1	6	60	7	1	8	1037	9	229	10	222
158	3	1	5	2	6	60	7	1	8	1037	9	229	10	222
159	3	1	5	3	6	60	7	1	8	1037	9	229	10	222
160	3	1	5	1	6	60	7	2	8	1037	9	229	10	222
161	3	1	5	2	6	60	7	2	8	1037	9	229	10	222
162	3	1	5	3	6	60	7	2	8	1037	9	229	10	222
163	3	1	5	1	6	60	7	3	8	1037	9	229	10	222
164	3	1	5	2	6	60	7	3	8	1037	9	229	10	222
165	3	1	5	3	6	60	7	3	8	1037	9	229	10	222
166	3	1	5	1	6	60	7	4	8	1037	9	229	10	222
167	3	1	5	2	6	60	7	4	8	1037	9	229	10	222
168	3	1	5	3	6	60	7	4	8	1037	9	229	10	222
169	3	1	5	1	6	90	7	1	8	1454	9	321	10	316
170	3	1	5	2	6	90	7	1	8	1454	9	321	10	316
171	3	1	5	3	6	90	7	1	8	1454	9	321	10	316
172	3	1	5	1	6	90	7	2	8	1454	9	321	10	316
173	3	1	5	2	6	90	7	2	8	1454	9	321	10	316
174	3	1	5	3	6	90	7	2	8	1454	9	321	10	316
175	3	1	5	1	6	90	7	3	8	1454	9	321	10	316
176	3	1	5	2	6	90	7	3	8	1454	9	321	10	316
177	3	1	5	3	6	90	7	3	8	1454	9	321	10	316
178	3	1	5	1	6	90	7	4	8	1454	9	321	10	316
179	3	1	5	2	6	90	7	4	8	1454	9	321	10	316
180	3	1	5	3	6	90	7	4	8	1454	9	321	10	316
181	4	1	5	1	6	15	7	1	8	232	9	49	10	48
182	4	1	5	2	6	15	7	1	8	232	9	49	10	48
183	4	1	5	3	6	15	7	1	8	232	9	49	10	48
184	4	1	5	1	6	15	7	2	8	232	9	49	10	48
185	4	1	5	2	6	15	7	2	8	232	9	49	10	48
186	4	1	5	3	6	15	7	2	8	232	9	49	10	48
187	4	1	5	1	6	15	7	3	8	232	9	49	10	48
188	4	1	5	2	6	15	7	3	8	232	9	49	10	48
189	4	1	5	3	6	15	7	3	8	232	9	49	10	48
190	4	1	5	1	6	15	7	4	8	232	9	49	10	48
191	4	1	5	2	6	15	7	4	8	232	9	49	10	48
192	4	1	5	3	6	15	7	4	8	232	9	49	10	48
193	4	1	5	1	6	45	7	1	8	649	9	141	10	142
194	4	1	5	2	6	45	7	1	8	649	9	141	10	142
195	4	1	5	3	6	45	7	1	8	649	9	141	10	142
196	4	1	5	1	6	45	7	2	8	649	9	141	10	142
197	4	1	5	2	6	45	7	2	8	649	9	141	10	142
198	4	1	5	3	6	45	7	2	8	649	9	141	10	142
199	4	1	5	1	6	45	7	3	8	649	9	141	10	142
200	4	1	5	2	6	45	7	3	8	649	9	141	10	142
201	4	1	5	3	6	45	7	3	8	649	9	141	10	142
202	4	1	5	1	6	45	7	4	8	649	9	141	10	142
203	4	1	5	2	6	45	7	4	8	649	9	141	10	142
204	4	1	5	3	6	45	7	4	8	649	9	141	10	142
205	4	1	5	1	6	60	7	1	8	818	9	164	10	194
206	4	1	5	2	6	60	7	1	8	818	9	164	10	194
207	4	1	5	3	6	60	7	1	8	818	9	164	10	194
208	4	1	5	1	6	60	7	2	8	818	9	164	10	194
209	4	1	5	2	6	60	7	2	8	818	9	164	10	194

Appendix 6 cont:

210	4	1	5	3	6	60	7	2	8	818	9	164	10	194
211	4	1	5	1	6	60	7	3	8	818	9	164	10	194
212	4	1	5	2	6	60	7	3	8	818	9	164	10	194
213	4	1	5	3	6	60	7	3	8	818	9	164	10	194
214	4	1	5	1	6	60	7	4	8	818	9	164	10	194
215	4	1	5	2	6	60	7	4	8	818	9	164	10	194
216	4	1	5	3	6	60	7	4	8	818	9	164	10	194
217	4	1	5	1	6	90	7	1	8	1119	9	236	10	239
218	4	1	5	2	6	90	7	1	8	1119	9	236	10	239
219	4	1	5	3	6	90	7	1	8	1119	9	236	10	239
220	4	1	5	1	6	90	7	2	8	1119	9	236	10	239
221	4	1	5	2	6	90	7	2	8	1119	9	236	10	239
222	4	1	5	3	6	90	7	2	8	1119	9	236	10	239
223	4	1	5	1	6	90	7	3	8	1119	9	236	10	239
224	4	1	5	2	6	90	7	3	8	1119	9	236	10	239
225	4	1	5	3	6	90	7	3	8	1119	9	236	10	239
226	4	1	5	1	6	90	7	4	8	1119	9	236	10	239
227	4	1	5	2	6	90	7	4	8	1119	9	236	10	239
228	4	1	5	3	6	90	7	4	8	1119	9	236	10	239

Variables 1-4 (column 2) are the dates on which the pats were exposed: 1 = 5 May; 2 = 19 June; 3 = 3 August; 4 = 17 September.

Variable 5 (column 4) indicates the position of the pat within the stratified random block: 1 was at the bottom of a slight slope, and 3 was at the top.

Variable 6 (column 6) is the number of days for which the pat was exposed.

Variable 7 (column 8) indicates the level of ivermectin (mg/kg) initially applied to the pat: 1 = 2; 2 = 1; 3 = 0.5; 4 = 0.

Variable 8 (column 10) is the Accumulated Temperature (^{o}C) that the pat was exposed to. For each day on which the pat was exposed the 'daily temperature' was calculated as: $^{(max + min)}/_{2}$ + 4. The Accumulated Temperature is the sum of all the 'daily temperatures' over the exposure period.

Variable 9 (column 12) is the Accumulated Rainfall (mm) that the pat was exposed to.

Variable 10 (column 14) is the Accumulated Hours of Sunshine that the pat was exposed to.

APPENDIX 7. Taxa abundances in the soil samples from below each of the experimental cow pats. Taxa numbers (Table 8.2) with corresponding abundance values are shown for each sample number (Table 8.1).

001	36	15	37	1	53	8	59	1	63	2				
002	19	2	34	1	36	6	53	4	63	1				
003	10	1	19	1	25	1	35	2	36	11	37	1	39	1
003	45	1	51	1	53	3	63	4						
004	35	2	36	3	37	2	49	1	53	2				
005	19	1	21	1	35	1	37	1	42	2	53	3	54	1
006	25	1	35	1	36	1	37	3	42	1	53	12		
007	19	1	37	4	53	3								
008	19	2	21	1	36	2	37	2	53	6	63	1		
009	03	4	19	2	25	4	29	1	34	1	37	6	38	1
009	42	1	53	33	54	2	63	1						
010	02	9	11	1	19	2	25	6	26	12	30	1	32	2
010	42	1	53	7										
011	02	3	19	1	24	1	25	12	26	19	29	2	37	1
011	51	1	53	17	63	2								
012	02	1	03	2	19	1	25	4	26	44	29	1	32	5
012	37	4	53	20	54	1	63	2						
013	19	1	32	2	36	1	63	5						
014	32	2	53	1	63	5								
015	25	1	43	1	53	2	63	6						
016	32	2	35	1	36	3								
017	19	1												
018	63	6												
019	32	1	63	1										
020	32	1	53	2	58	1								
021	25	1	53	4	63	3								
022	25	3	63	1										
023	25	44	32	6	53	2	62	2	63	2				
024	02	2	25	76	29	3	32	2	63	4				
025	32	1	63	1										
026	53	1	58	1	63	3								
027	32	2	53	1	63	1								
028	32	1	64	1										
029	32	4	36	2										
030	32	1	35	2	37	1	64	1						
032	19	1	32	1	63	1								
033	19	1	32	1	63	1								
034	25	10	32	1	53	1	56	1						
035	19	1	32	2	35	1	63	3						
036	29	1	32	7	53	1								
037	61	1	63	3										
038	63	1												
039	63	1	65	1										
042	32	2	35	1										
043	19	2	61	1	63	1								
044	19	1	32	1	53	1	63	1						
045	32	1	63	1	64	2								
046	25	3	63	2										
047	20	4	25	1	26	4	29	2	32	16	63	1	64	1
048	25	3	32	6	53	1								
049	58	1	63	6										
050	63	4												
051	63	2												
052	63	4												
053	63	4												

Appendix 7 cont:

054	63	3												
055	63	13												
057	33	1	63	2										
058	32	1	63	6										
059	63	9												
060	63	3												
061	63	1												
062	20	14	53	7	63	3								
063	19	1	32	2	35	1	36	2	52	1	53	2	63	1
064	17	1	34	1	53	1								
065	32	1	43	3	52	1	53	2						
066	20	1	32	1	53	2								
067	24	1	52	1	53	2	63	1	64	2				
068	20	56	32	4	53	2	63	1						
069	63	1	64	2										
070	02	1	24	2	32	2	43	1	53	5				
071	02	3	19	1	24	1	29	1	30	1	32	1	53	1
071	63	2												
072	12	2	24	1	29	2	53	15	54	1	64	2		
073	63	6												
074	63	1												
075	19	1	63	3										
076	63	2												
077	20	17	63	2										
078	43	1	63	7										
079	63	4												
080	63	7												
081	43	1	63	3										
082	32	1	63	5										
083	63	2												
084	07	4	63	3										
085	63	6												
086	53	1	63	3										
087	63	4												
088	63	6												
089	43	1	53	1	63	9								
090	58	1	63	4										
091	63	10												
092	63	4												
093	07	2	53	1	63	12								
094	07	7	11	1	32	1	63	6						
095	07	32												
096	07	21	63	7										
097	63	6												
098	63	5												
099	63	4												
100	63	5												
101	63	3												
102	63	7												
103	07	1	33	1	63	6								
104	07	2	63	6										
105	34	1	63	4										
106	07	1	63	6										
107	07	8	63	9										
108	07	1	33	1	58	1	63	5						
109	63	1												
110	63	1												
111	63	1												
112	19	1												

Appendix 7 cont:

113	63	6						
114	63	3						
115	63	2						
116	63	1						
117	63	6						
118	63	2						
119	63	1						
120	63	2						
121	63	2						
122	63	2						
124	34	5	63	1				
125	63	1						
126	34	1	63	1				
127	63	2						
128	63	1						
129	31	8	63	2				
130	10	3	21	1	32	1	63	1
131	32	1	34	1				
132	31	1	63	3				
133	63	3						
134	63	8						
135	63	3						
136	63	4						
137	63	11						
138	63	4						
139	33	1	63	2				
140	63	10						
141	63	4						
142	31	2	63	7				
143	14	1	31	5	63	6		
144	31	1	63	9				
145	63	3						
146	63	12						
147	63	6						
148	63	2						
149	63	3						
150	63	3						
151	63	7						
152	63	5						
153	63	6						
154	11	1	31	4	53	1	63	10
155	05	1	63	8				
156	63	5						
157	63	3						
158	63	5						
159	63	1						
160	63	1						
161	63	1						
162	63	5						
163	63	7						
164	63	1						
165	63	1						
166	63	4						
167	63	2						
168	63	4						
169	63	2						
170	33	1						
171	63	1						
172	63	2						

Appendix 7 cont:

173	64	2						
174	63	2						
175	63	2						
176	63	1						
177	63	1						
178	33	1	63	3				
179	53	1	63	2				
180	31	1	63	3				
181	63	2						
182	21	3	63	1				
183	49	5	63	2				
184	53	1	63	1				
185	38	1	49	1	53	1	63	1
186	34	1	49	1	53	1	63	1
187	63	2						
188	46	1	47	1	63	1		
189	63	2						
190	63	1						
191	49	1	53	1	63	1		
192	49	1	63	2				
193	22	1	63	4				
194	63	1						
195	63	1						
197	21	1						
198	63	3						
199	21	2	63	2				
200	63	2						
201	63	1						
202	39	1	63	3				
203	63	3						
204	05	2						
205	63	2						
206	63	3						
207	63	1						
208	63	1						
209	63	3						
210	34	1	63	1				
211	63	4						
212	63	2						
213	63	4						
214	19	1	63	2				
215	05	1	34	1	63	2		
216	63	2						
217	63	1						
218	63	2						
222	63	1						
225	63	1						
226	63	1						